
SYSTEMATICS OF THE AMAZON LILIES, *EUCHARIS* AND *CALIPHRURIA* (AMARYLLIDACEAE)¹

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ABSTRACT

Eucharis and *Caliphruria* are closely related, neotropical genera of petiolate-leaved, white-flowered Amaryllidaceae found in the understory of primary tropical rain forest. Together with the Peruvian endemic *Urceolina*, *Eucharis* and *Caliphruria* form a monophyletic group within "infrafamily Pancratioidinae" on the basis of leaf and seed morphology and ecological specialization. Seventeen species and two natural hybrids within two subgenera are recognized in *Eucharis*. *Eucharis*, marked by its crateriform or campanulate flowers, curved perianth tube, pigmented androecium usually developed into a staminal cup, and unicellular stigmatic papillae, is distributed from Guatemala to Bolivia, chiefly in the western Amazon basin and adjacent lower slopes of the eastern Andes. Subgenus *Heterocharis* represents three relict species and two natural hybrids with many ancestral characters of the genus. *Caliphruria* (four species, three of which are endemic to Colombia) has funnellform flowers, straight perianth tube, reduced staminal connation, and multicellular stigmatic papillae. Cladistic relationships support the monophyly of *Eucharis*, *Caliphruria*, and *Urceolina* as a unified group. The most parsimonious cladograms suggest that *Eucharis* is paraphyletic if subg. *Heterocharis* is included. An alternative hypothesis of generic relationships is tested, and proves less parsimonious. Recognizing the close phenetic relationship of subg. *Heterocharis* to the rest of *Eucharis*, the high levels of homoplasy within the cladogram, and ambiguity caused by missing character state data, a less parsimonious phylogeny is accepted as the basis for classification. Keys and descriptions are provided for all species of *Eucharis* and *Caliphruria*. *Eucharis caucana*, a novel hexaploid ($2n = 138$) species, is described from Colombia.

The closely related genera *Eucharis* Planchon & Linden and *Caliphruria* Herbert (Amaryllidaceae), the Amazon lilies, comprise respectively 17 and 4 species of bulbous, rain forest geophytes adapted to the low light conditions of the forest understory. Together with the Peruvian endemic *Urceolina* Reichenb., nom. cons., *Eucharis* and *Caliphruria* form a monophyletic group delimited by petiolate leaves with distinctive cuticular striation; a turgid seed with a lustrous, usually black testa; and complete fidelity to the rain forest under-

story niche. The species are distributed from Guatemala to Bolivia. The major center of distribution for *Eucharis* is in the western Amazon basin (inclusive of major tributary systems, e.g., the Napo, Pastaza, and Huallaga) and the adjoining lower slopes of the eastern Andean cordillera. With the exception of single Peruvian species, *Caliphruria* is restricted to the Cordillera Occidental and Cordillera Central of Colombia. The species of both genera are nowhere abundant, and are found growing only in primary, rarely secondary, forest from

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Mazama gouazoubira as an incorrect subsequent spelling and *M. gouazoupira* (Fischer, 1814) as the correct original spelling, though I would agree that this was not a positive contribution to stability. However, until recently there was no procedure to conserve a preferred emendation other than by appealing to the Commission. This Gardner has now done, and very clearly. He should be supported.

The new Code (4th Edition), laying clearer emphasis on stability, renders these exercises unnecessary in the future by providing a firm distinction between a nomen oblitum and a nomen protectum (Article 23.9): between the original but almost universally rejected or ignored spelling and the generally accepted spelling. One will no longer see the unsupported statement that an original spelling is a lapsus in such examples as the following: *Tadarida teniotis rueppellii* (*Dysopes rüppelii* Temminck, 1826), *Callicebus brunneus* (*Callithrix brunea* Wagner, 1842), *Procolobus badius temminckii* (*Colobus temminckii* Kuhl, 1820), *Vulpes rueppellii* (*Canis rüppelii* Schinz, 1825), *Hendecapleura* (*Endecapleura* Lataste, 1882), and *Myomyscus verreauxi* (*Mus verroxii* A. Smith, 1834). These emendations are likely to be nomina protecta. Perhaps it is worth indicating that a correction to spelling in itself is not necessarily going to become a nomen protectum: Rosevear's (1969, p. 201) emendation of *Tatera welmanni* (*Taterona welmanni* St Leger, 1929) to *T. welmani* on the grounds that the taxon was named after J.B. Welman has not been supported in the literature, and there is no move to emend *Equus chapmani* Layard, 1865, named after J. Chapman. Clear distinctions must be made between (a) misspelled names whose status has not been challenged and which should remain valid; (b) neglected original spellings whose restoration has not been challenged; (c) widely used emendations which become nomina protecta under the new Code; and (d) rational emendations which have not been adopted in the literature and therefore remain unjustified.

Additional references

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Comment on the proposed conservation of LORISIDAE Gray, 1821 and GALAGIDAE Gray, 1825 (Mammalia, Primates) as the correct original spellings
(Case 3004; see BZN **55**: 165-168; **56**: 73; **57**: 51)

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In their request to the Commission to reject our proposal to conserve LORISIDAE and GALAGIDAE as the correct original spellings, Groves & Jenkins (BZN 57: 51, March 2000) rest their argument on the use of LORIDAE and GALAGONIDAE in 'at least four influential works' that appeared subsequent to Jenkins's (1987) resurrection of the latter two family names. One of these publications (McKenna & Bell, 1997) would have incorporated the names LORISIDAE and GALAGIDAE had the application, which was submitted in 1995, not been delayed by other matters before the Commission. But, more importantly, we suggest that if the spirit of the Code to maintain stability is to be upheld, LORISIDAE and GALAGIDAE should be conserved as the correct original spellings not only for the reason, as we demonstrated in our original proposal, that with extremely minor exceptions these have been the predominant spellings in the primatological literature, but also because they continue to be the forms used in those recent publications that are and will have the most impact on current and future students of primates. Since Jenkins's (1987) publication, LORISIDAE and GALAGIDAE (and/or LORISINAE and GALAGINAE) have been used, for example, by Martin (1990), Conroy (1990), Fleagle (1988, which was replaced by Fleagle, 1999), Delson et al. (2000, which superseded Tattersall et al., 1988), and Ankel-Simons (2000), all of which constitute primary sources for both the teaching and research activities of those who specialize in primate studies, which span the gamut from systematics to paleontology, ecology and behavior. The widespread use of these influential works in teaching at the undergraduate as well as graduate level in the production of future generations of primate specialists adds further to the need to maintain stability in nomenclature. We should also mention that LORISIDAE and GALAGIDAE (and/or LORISINAE and GALAGINAE) remain in use in the nine most popular undergraduate textbooks in biological and physical anthropology. In addition, Nowak (1999), which is a standard reference work on living mammals, continues the long-standing tradition of recognizing these familiar family-group names. Of course, this discussion does not include the many articles published since 1987 that use these family (and/or subfamily) names.

The Commission is requested to accept our proposal.

As for the spellings of the names for other primate groups that Groves & Jenkins mention, INDRIDAE (for 'INDRIIDAE'), STREPSIRRHINI (for 'STREPSIRHINI') and HAPLORRHINI (for 'HAPLORHINI'), we purposefully chose not to include discussion of them in our original proposal in order not to complicate matters. We had intended to bring these issues before the Commission following our original proposal. Since, however, Groves & Jenkins have now introduced these items, we must point out that all but one of the primate reference works cited above that continue the tradition of using LORISIDAE and GALAGIDAE (and/or LORISINAE and GALAGINAE) also continue the tradition of using STREPSIRHINI, HAPLORHINI and INDRIDAE as the correct spellings. In addition, in his widely used human evolution text, Conroy (1997) maintains the spellings STREPSIRHINI and HAPLORHINI in his background review of the major subdivisions of Primates. Thus, the arguments we made in our original proposal as well as here to preserve LORISIDAE and GALAGIDAE also apply to the conservation of STREPSIRHINI, HAPLORHINI and INDRIDAE as the correct spellings.

Additional references

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- Fleagle, J.G. 1999. *Primate adaptation and evolution*, Ed. 2. Academic Press, New York.
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It tends toward subterete cross sections (Fig. 1), rounded abaxially, and flattened adaxially, becoming slightly channeled proximal to the sinus. The petiole is winged proximal to the sinus by attenuation of the lamina. The midrib is pronounced abaxially along the entire length of the lamina, and slightly channeled adaxially, continuous with the petiole.

Leaf shape only rarely provides taxonomically useful information. Length/width ratios are subject to considerable variation even among the leaves of a single bulb. Herbarium specimens will frequently include only a single leaf, with no indication of its developmental age. Taxonomic consistency of leaf shape is exceptional, but useful in the few cases where it occurs. For example, leaves of *E. ulei* Kränzlin are consistently narrowly elliptic. *Eucharis amazonica* (leaf length/width ratio greater than 2) may be delimited from *E. moorei* (Baker) Meerow (l/w less than 2).

The leaves of *Eucharis* and *Caliphruria* are completely glabrous and nonglaucous, with a single exception. *Eucharis bonplandii* (Kunth) Traub, a rare tetraploid species from central Colombia, develops a glaucous bloom that gives the leaf a blue cast in strong light.

The leaf apex of all species is shortly acuminate, the base attenuate. Coarse undulation of the margin will sometimes make the lamina appear cordate at the base. Leaf margins of *Caliphruria* are uniformly nonundulate.

Leaf venation of *Eucharis* and *Caliphruria* is parallelodromous (Hickey, 1973), with a great number of transverse, commissural veins interconnecting the primary vasculature. All species of *Caliphruria* have smooth, nonplicate leaves. *Eucharis* is variable for this character, but the majority of species have plicate leaves.

The adaxial epidermis of most species of both genera is lustrous, dark green; the abaxial surface appears lighter, or silvery green. Only *E. astrophia* (Ravenna) Ravenna has diverged markedly from the typical morphology and has a uniquely nonlustrous, bullate-pustulate leaf texture.

CUTICLE

Cuticular striation is prominent on the abaxial leaf surfaces of most *Eucharis* and *Caliphruria* species (Figs. 2–6, 8–12). Striae are thickest in *C. subdentata* (Fig. 11). Arroyo & Cutler (1984) recognized eight cuticular sculpturing classes in a survey of 25 genera of Amaryllidaceae. The most common cuticular morphology of *Eucharis* and *Caliphruria* fits their class VII: “thick striae, parallel or not, interlocking, \pm transverse.”

In a few species of *Eucharis* (*E. amazonica*, *E. moorei* (Fig. 10), *E. bouchei* (Fig. 9)), the striation is much less pronounced. *Caliphruria korsakoffii* (Traub) Meerow (the sole representative of *Caliphruria* outside Colombia) has the most aberrant cuticle morphology (Fig. 12), corresponding more or less to type V of Arroyo & Cutler (1984): “central, thick axial striation with less pronounced striae running from it, directly to anticlinal walls.” The adaxial cuticles of *Eucharis* and *Caliphruria* are either smooth or rarely much more finely striate than the abaxial surface, the striations entirely axial in orientation. The adaxial cuticle of *C. korsakoffii* (Fig. 13) has several, thick, transverse striations across each cell, and the epidermis is unusually flat.

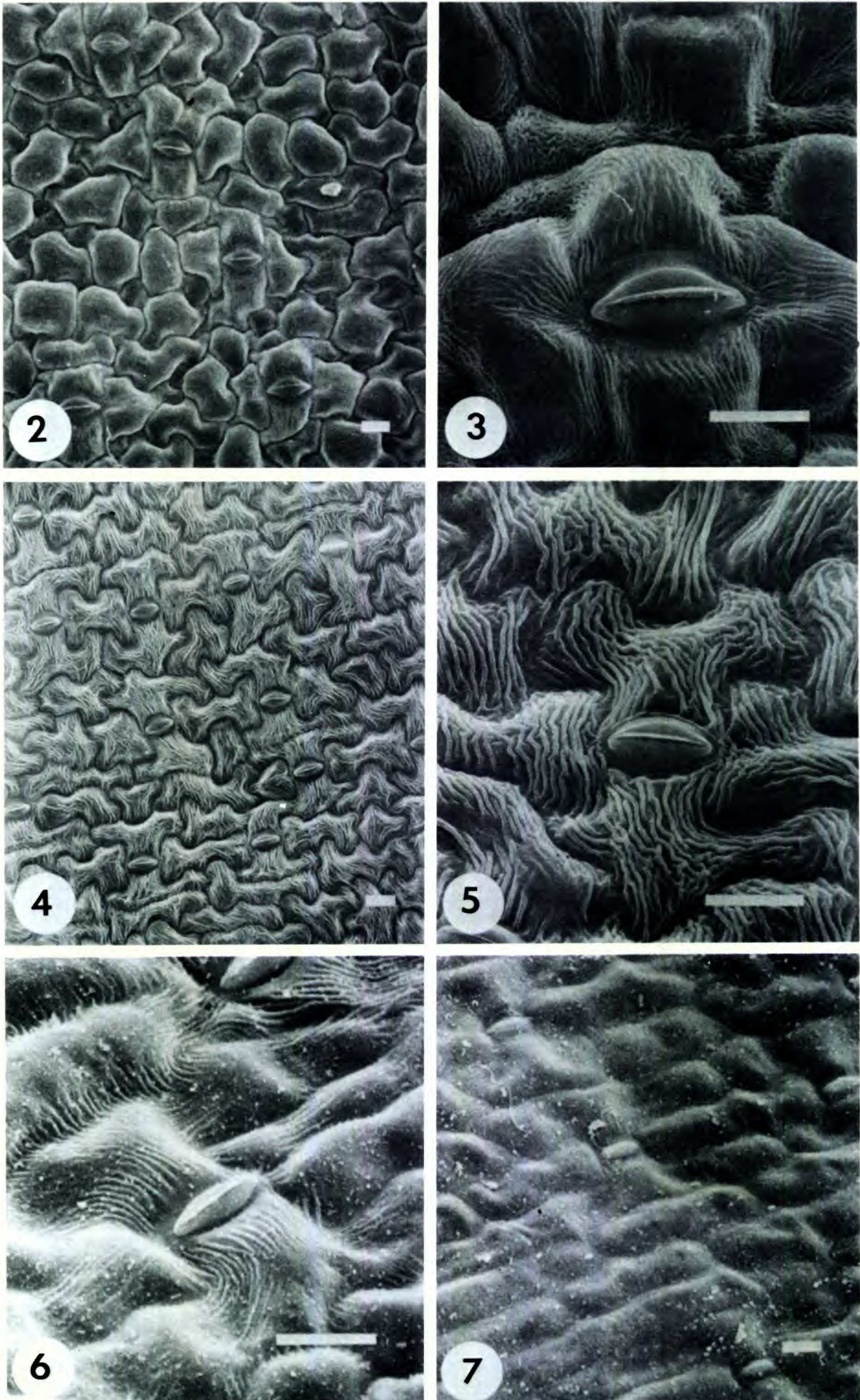
STOMATA

Leaves of *Eucharis* and *Caliphruria* are predominantly hypostomatic. Stomata occur adaxially only along the midrib and vicinity (Fig. 14A), and occasionally in the proximity of primary veins. Stomata are usually absent from the abaxial midrib (Fig. 14B). Intercalary stomata were regularly observed only in *E. cyaneosperma* Meerow (Figs. 7, 15D). The stomata of *Eucharis* and *Caliphruria* are anomocytic, as is typical for Amaryllidaceae (Arroyo & Cutler, 1984; Dahlgren & Clifford, 1982), though *E. astrophia* exhibits at least slight differentiation of cells neighboring the stomata (Figs. 2, 3) from other epidermal cells. These cells are more densely and regularly striate than other epidermal cells, as well as slightly more raised. The guard cells of *Eucharis* and *Caliphruria* are oriented with their longest axis parallel to that of the leaf.

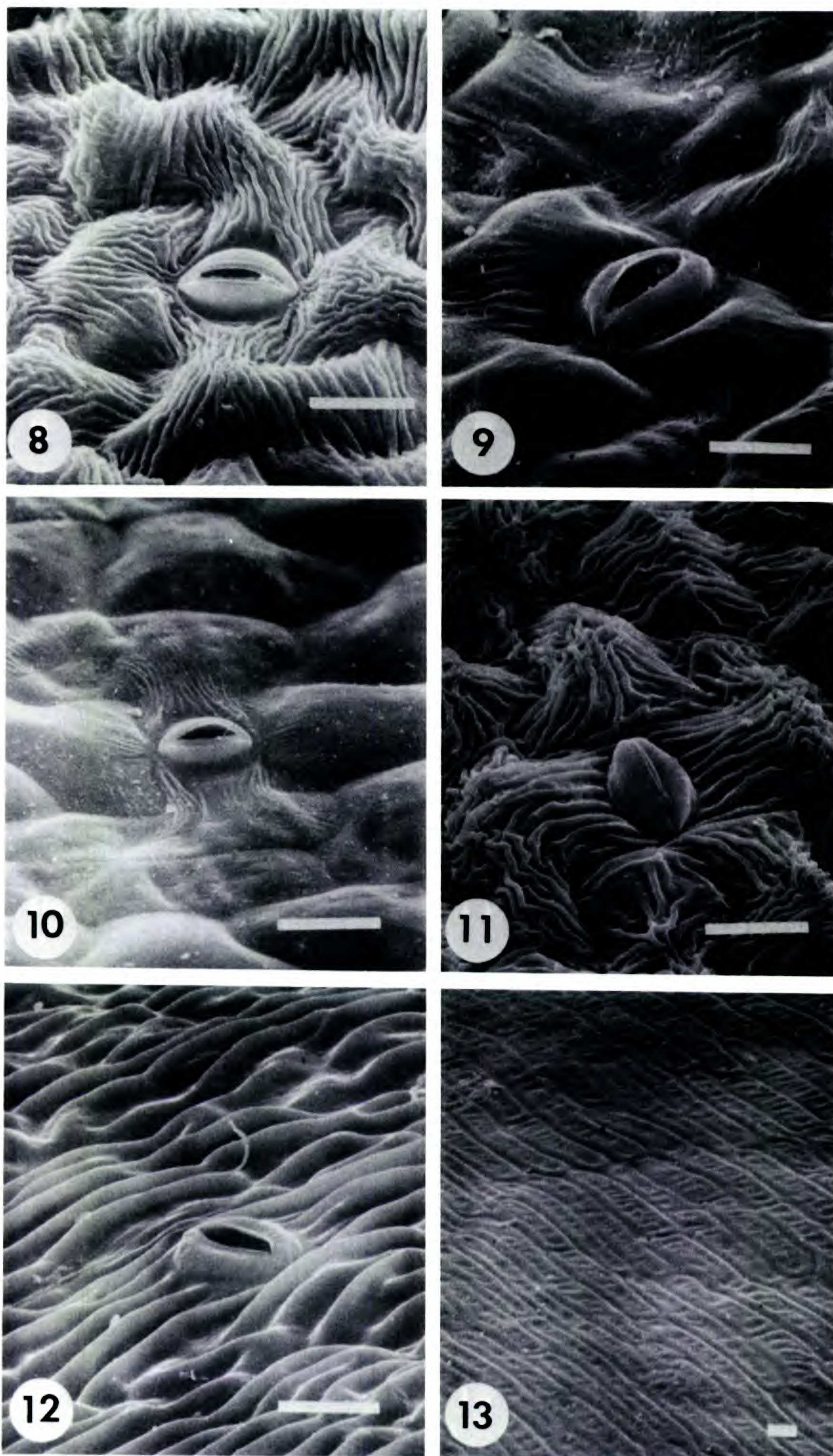
EPIDERMAL CELLS

Abaxial epidermal cells range from rectangular to irregular in shape. Adaxial epidermal cells are in almost all cases rectangular. *Eucharis astrophia* (Fig. 15A) has the most irregularly shaped cells of both the abaxial and adaxial surfaces. In the vicinity of the midrib on both surfaces of the leaf (Fig. 14), epidermal cells become conspicuously elongated, and anticlinal walls are straight. Epidermal cells of the midrib are extremely long and narrow.

The epidermal cells of all species of *Eucharis* subg. *Eucharis* have strongly undulate anticlinal walls (Fig. 15), as noted by Asatrian (1984) for the few species he surveyed. End walls of both the abaxial and adaxial cells of all species range from oblique to rounded. Abaxial cells are more strongly



FIGURES 2-7. SEM photomicrographs of *Eucharis* leaf surfaces. 2-6. Abaxial leaf surfaces.—2, 3. *E. astrophiala* (Meerow 1111, FLAS).—4, 5. *E. plicata* subsp. *plicata* (Meerow 1025, FLAS).—6. *E. cyaneosperma* (Meerow 1032, FLAS).—7. Adaxial leaf surface of *E. cyaneosperma* (Meerow 1032, FLAS). All scales = 25 μm .



FIGURES 8-13. SEM photomicrographs of *Eucharis* and *Caliphruria* leaf surfaces. 8-12. Abaxial surfaces.—8. *E. bakeriana* (Meerow 1108, FLAS).—9. *E. bouchei* var. *dressleri* (Meerow 1107, FLAS).—10. *E. moorei* (Meerow 1141, FLAS).—11. *C. subdentata* (Meerow 1109, FLAS).—12. *C. korsakoffii* (Meerow 1096, FLAS).—13. Adaxial surface of *C. korsakoffii* (Meerow 1096, FLAS). All scales = 25 μm .

undulate than those of the adaxial surface. Epidermal cells of *Caliphruria* (Fig. 15F) are more weakly undulate than those of *Eucharis*. The anticlinal walls of adaxial cells of *C. korsakoffii* are completely straight. *Eucharis* subg. *Heterocharis* is polymorphic for anticlinal wall morphology. *Eucharis amazonica* and *E. sanderi* have strongly undulate walls, while *E. moorei* (Fig. 15E) has essentially straight walls.

LEAF ANATOMY

In petiolar transverse section, a single arc of vascular bundles is usually observed (Fig. 1). Median bundles are the largest. In petioles of *E. moorei* (Fig. 1E) and the closely related *E. amazonica* (Fig. 1F), both in subg. *Heterocharis*, small secondary bundles were observed near the adaxial surface. These bundles are most conspicuous in *E. moorei*; they are markedly smaller in *E. amazonica*. These secondary vascular traces disappear above the middle of the petiole. Asatrian (1984), who reported on petiole anatomy of three *Eucharis* and *Caliphruria* species, did not observe these bundles in *E. amazonica* (cited as *E. grandiflora*).

The internal morphology of leaves of *Eucharis* and *Caliphruria* (Figs. 16–22) is largely invariant across both genera. No well-defined palisade layer is evident, the absence of which is characteristic of most genera of “infrafamily” Pancratioidinae (Arroyo & Cutler, 1984). Mucilage cells, common throughout the family (Arroyo & Cutler, 1984), are often present near the leaf surface, and raphides are occasionally observed in epidermal cells. The mesophyll consists of several layers of chlorenchyma both ad- and abaxially, and a thicker region of spongy, slightly aerenchymous tissue. Small air cavities occur regularly only directly below stomata. Vascular bundles are surrounded by a sheath of one or two layer(s) of parenchymous cells. The only xylem elements present are tracheids with annular thickenings (Fig. 19).

FLORAL MORPHOLOGY

INFLORESCENCE

The inflorescence of *Eucharis* and *Caliphruria* is a naked scape typical of Amaryllidaceae. The scape is subterete in cross section and has a solid pith. Vascular bundles are distributed in several irregular, concentric rings within the pith. A layer of collenchyma cells occurs just below the epidermis.

The scape is terminated by two valvate-imbricate, ovate-lanceolate bracts that enclose several

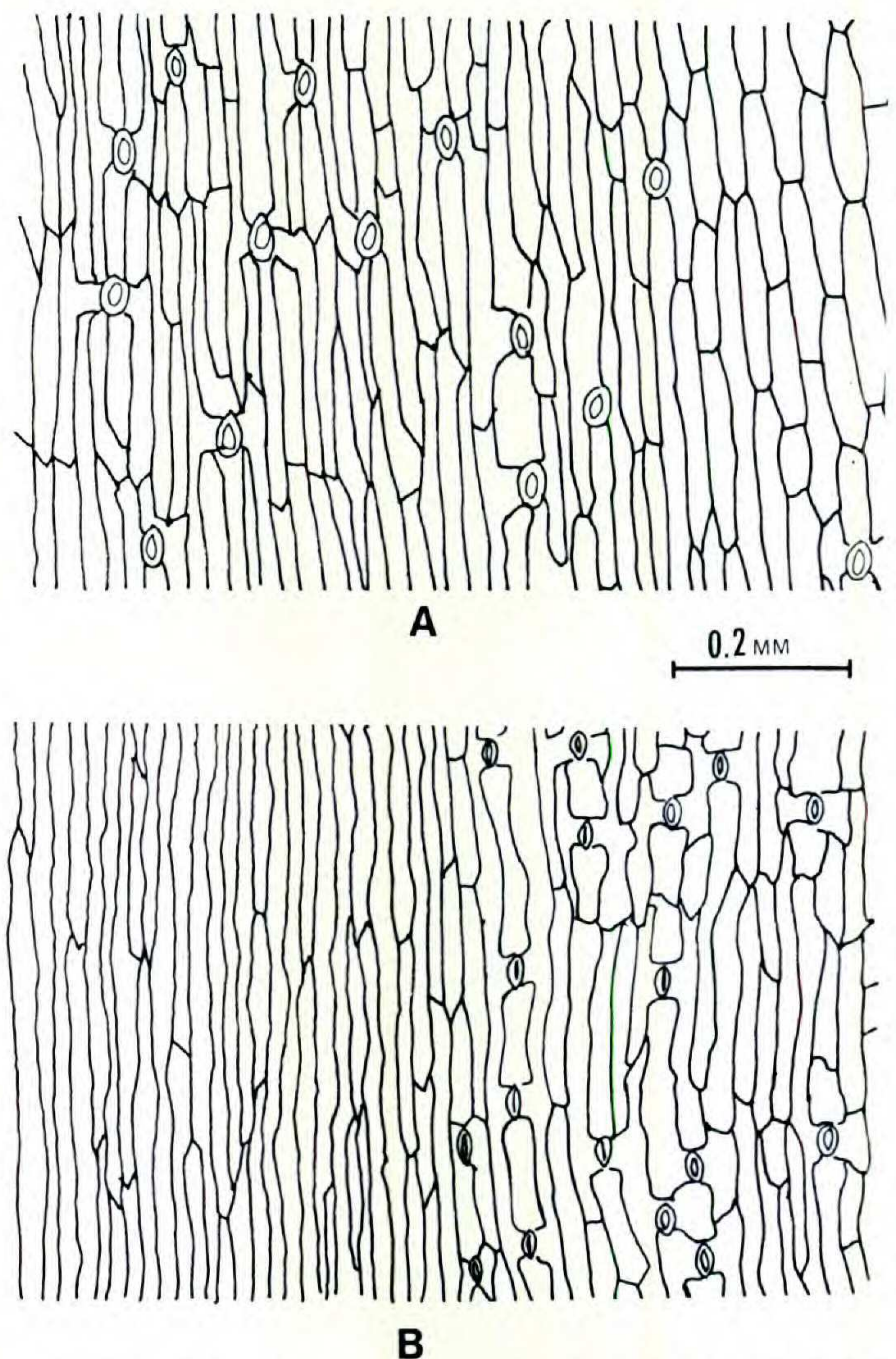


FIGURE 14. Leaf epidermal cell configurations in the vicinity of the midrib of representative *Eucharis* species.—A. *E. formosa* (Schunke 14174, FLAS), adaxial surface.—B. *E. plicata* subsp. *plicata* (Meerow et al. 1025, FLAS), abaxial surface.

secondary bracts and the flower buds before anthesis. These bracts vary from green (*E.* subg. *Heterocharis*) to greenish white (most species of subg. *Eucharis*) and are soon marcescent after opening and spreading laterally. Each flower is subtended by a linear-lanceolate bracteole.

The inflorescence of the Amaryllidaceae is traditionally described as “umbellate.” Mann (1959) and Stout (1944) demonstrated that the superficially simple umbel of Amaryllidaceae actually represents a complex series of reduced, helicoid cymes. Anthesis occurs in a strict sequence within each cyme from the developmentally oldest flower to the youngest. The peripheral cymes flower first; the central cymes flower last.

Flower number varies in *Eucharis* and *Caliphruria* from 2 to 10, rarely as many as 12 (*C. korsakoffii*, rarely in *E. castelnaeana*). Number of flowers is often a taxonomically useful character, though any species characterized by 8–10 flowers is capable of producing a depauperate inflorescence with fewer florets. An increase in flower number

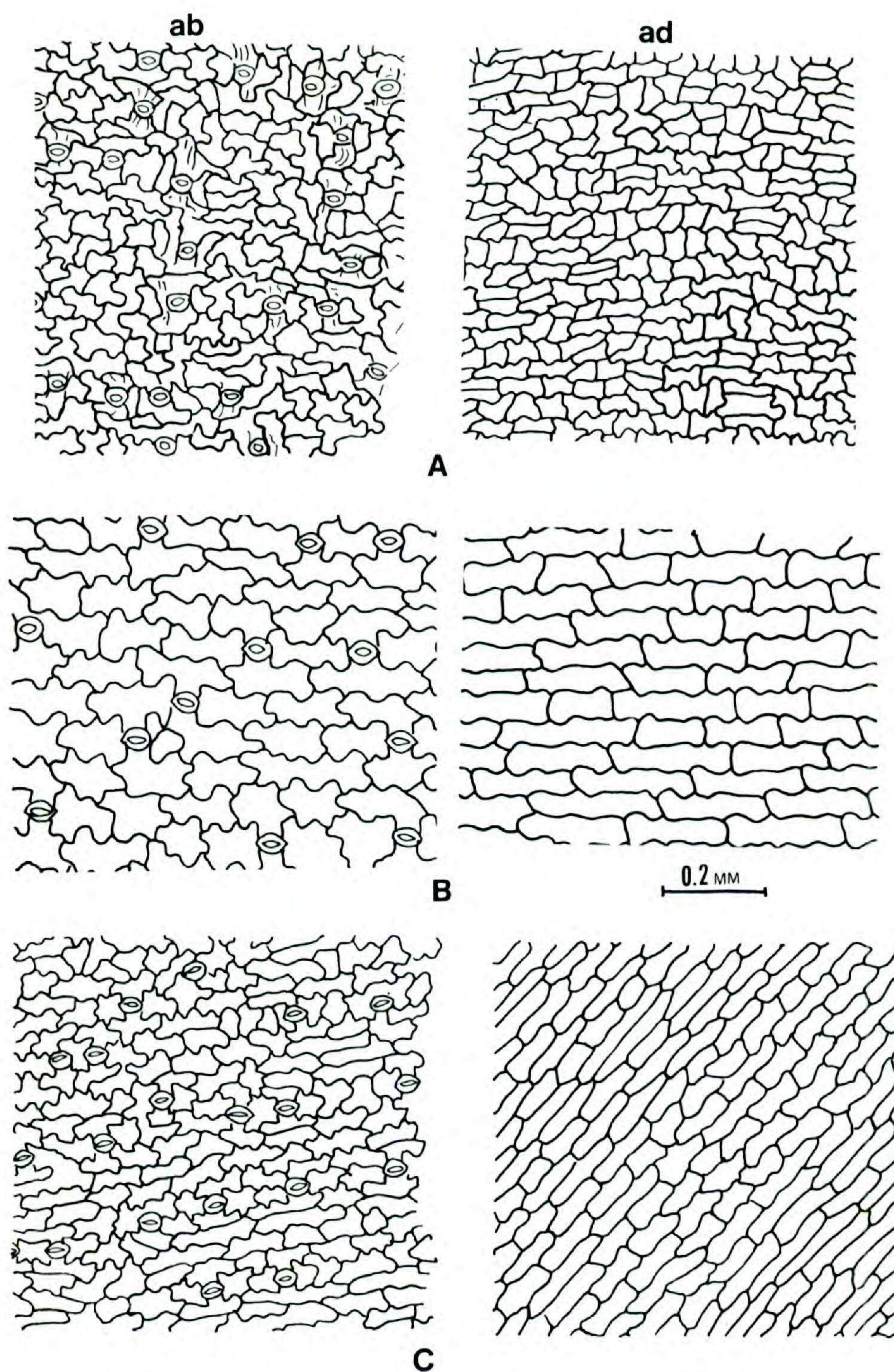


FIGURE 15A-C. Leaf epidermal configurations of representative *Eucharis* and *Caliphruria* species in the intercostal area of the leaf.—A. *E. astrophiala* (Madison 3792, SEL).—B. *E. bonplandii* (Bauml 686, HUNT).—C. *E. castelnaeana* (Schunke 14156, FLAS).

generally does not occur. In some species of subg. *Eucharis* (*E. astrophiala*, *E. bouchei*, *E. ulei*), a flower number of five has become virtually fixed. Reduction in flower number is usually considered the derived state in Amaryllidaceae (Traub, 1962, 1963).

FLOWER SIZE

The largest flowers in *Eucharis* are found in subg. *Heterocharis*, where they average 7–8 cm in length. Flowers of *Caliphruria* are the smallest, never exceeding 4 cm long. Subgenus *Eucharis*, the largest of the two subgenera of *Eucharis*, is

variable, with flowers 3–7 cm in length. Within a fairly broad range, flower size can be used to distinguish phenetic species complexes within subg. *Eucharis*; however, most species of this subgenus are quite variable in size (Meerow, 1987d, in press).

FLORAL FRAGRANCE

Subgenus *Heterocharis* is the only subgenus of *Eucharis* with uniformly fragrant flowers. The fragrance of all species of subg. *Heterocharis* is intense and sweet. Flowers of *Caliphruria* do not emit any detectable fragrance. Most species of *Eucharis* subg. *Eucharis* also lack noticeable fra-

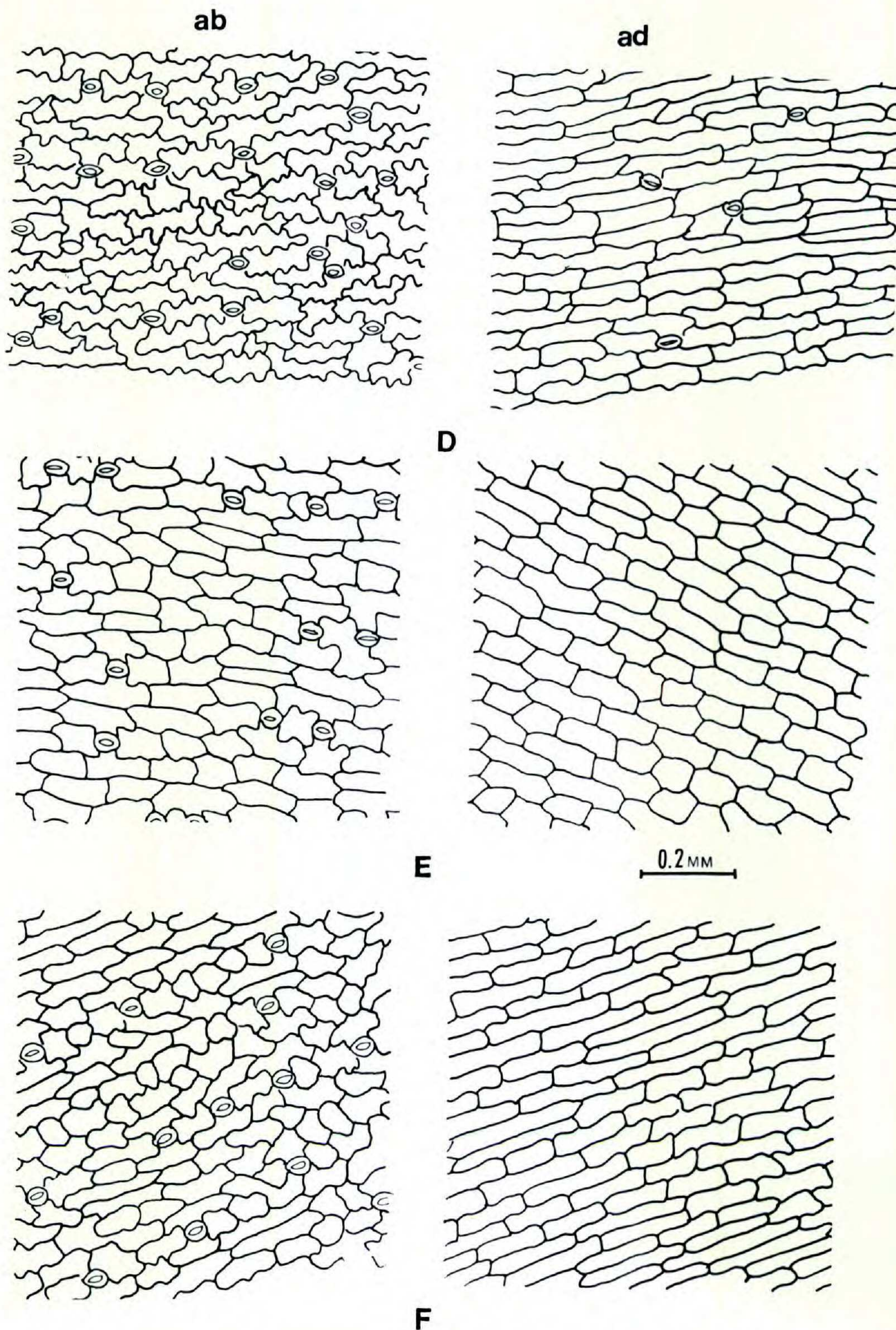


FIGURE 15D-F. Leaf epidermal configurations of representative *Eucharis* and *Caliphruria* species in the intercostal area of the leaf.—D. *E. cyaneosperma* (Meerow 1032, FLAS).—E. *E. moorei* (Meerow 1141).—F. *C. subedentata* (Meerow 1123, FLAS). ab = abaxial, ad = adaxial.

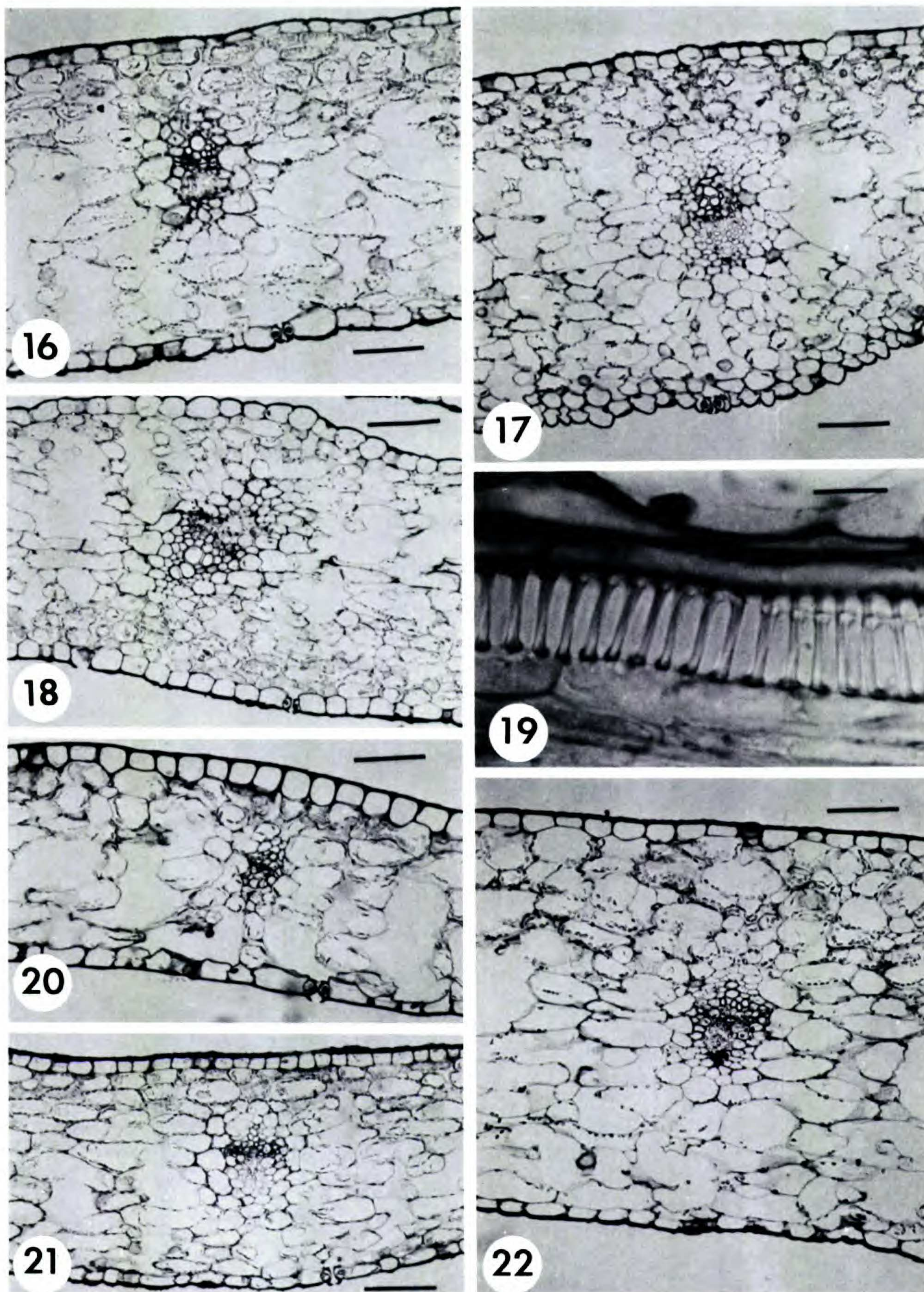
grance. In the few fragrant species of this subgenus (*E. bakeriana* N. E. Brown, *E. castelnaeana* (Bailon) Macbr., *E. formosa* Meerow, and *E. plicata* Meerow subsp. *brevidentata* Meerow), the odor is not intense. In *E. formosa* the odor is slightly fetid.

PERIANTH

The perianth of *Eucharis* and *Caliphruria* consists of six tepals in two whorls, basally connate into a tube of varying length and morphology. The tube of *Eucharis* subg. *Eucharis* (Fig. 23E) is

cylindrical for almost its entire length, abruptly dilating near the perianth throat. The tube of subg. *Eucharis* is also strongly curved, either abruptly just above the ovary (*E. bakeriana*, *E. cyaneosperma*) or gradually throughout the proximal half of its length (all other species). The curving of the tube results in the pendent habit of most species of subg. *Eucharis*. The tube is white for its entire length.

The tube of subg. *Heterocharis* (Fig. 23C, D) is tinted green proximally (for as much as half its length). The tube is curved, though not as markedly



FIGURES 16-22. Transverse sections of *Eucharis* and *Caliphruria* leaves.—16. *E. bonplandii* (Bauml 686, HUNT).—17. *E. astrophiala* (Madison 3792, SEL).—18, 19. *E. formosa* (Meerow 1103, FLAS). 19. Tracheid with annular thickenings.—20. *E. bouchei* var. *dressleri* (Meerow 1107, FLAS).—21. *C. subedentata* (Meerow 1123, FLAS).—22. *C. korsakoffii* (Meerow 1096, FLAS). All scales = 100 μm except 25 μm in Figure 19.

as that of subg. *Eucharis*, and the habit of the flowers is either declinate (*E. moorei*, *E. sanderi* Baker) or subpendulous (*E. amazonica*). The tube is cylindrical for $\frac{1}{2}$ to $\frac{2}{3}$ of its length; it abruptly

dilates in the distal $\frac{1}{2}$ to $\frac{1}{3}$. The tube morphology of \times *Calicharis butcheri* (Traub) Meerow (Fig. 23B), putatively an intergeneric hybrid between *E. sanderi* and *C. subedentata*, is intermediate be-

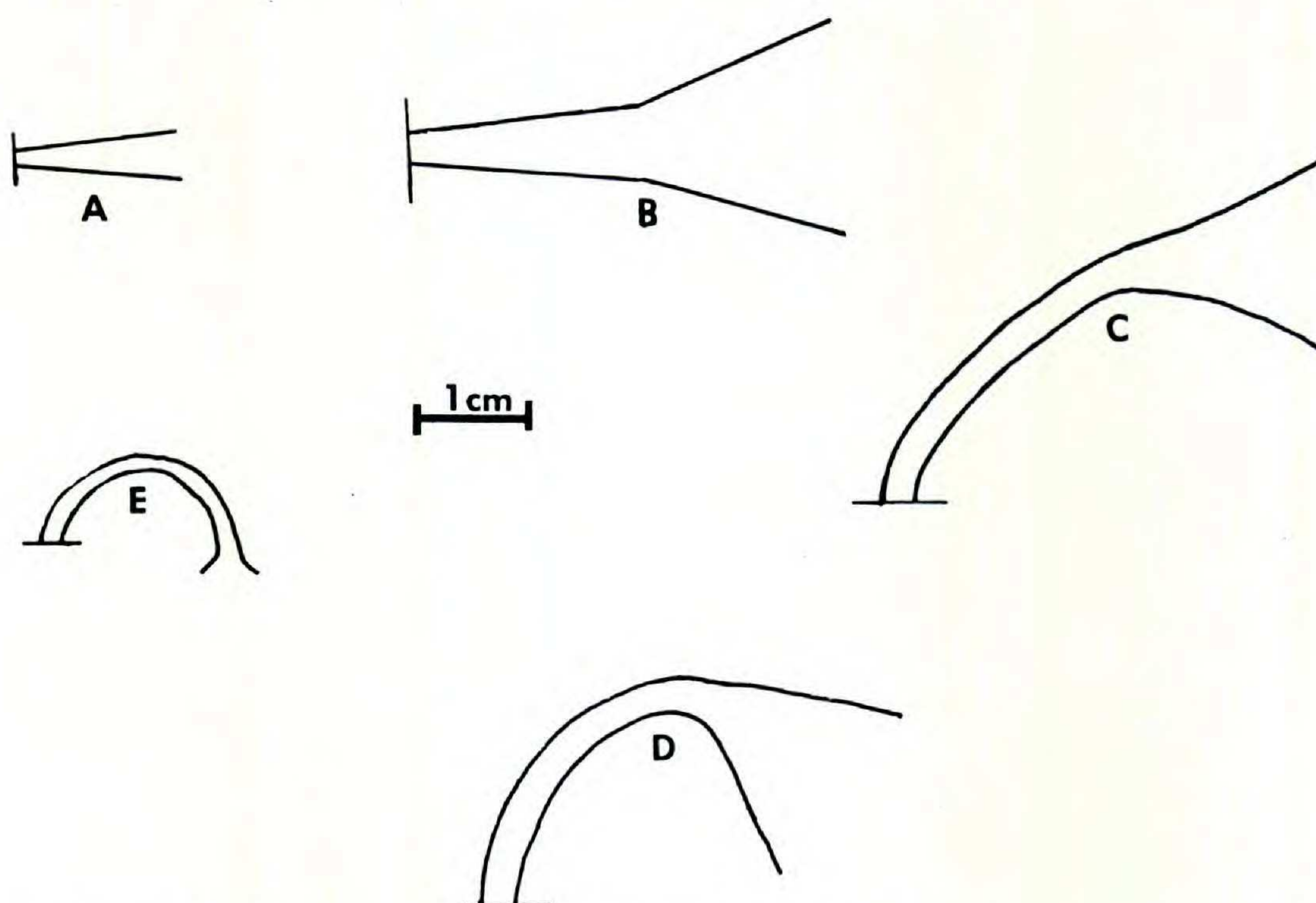


FIGURE 23. Perianth tube morphology of *Eucharis* and *Caliphruria* species or hybrids.—A. *C. subdentata* (Meerow 1098, FLAS).—B. \times *Caliphruria butcheri* (Meerow 1110, FLAS).—C. *E. sanderi* (Cuatrecasas 16380, F).—D. *E. amazonica* (Schunke 14179, FLAS).—E. *E. astrophiala* (Madison 3792, SEL).

tween *Caliphruria* (Fig. 23A) and *Eucharis* subg. *Heterocharis* (Fig. 23C, D).

The tube of *Caliphruria* (Fig. 23A) is straight and dilates gradually from base to throat. It is either subcylindrical (*C. korsakoffii*) or funnellform (all other species). The tube is tinted green proximally (in *C. subdentata*, for $\frac{1}{2}$ – $\frac{2}{3}$ of its length).

The tepals of *Eucharis* and *Caliphruria* flowers are white. Those of the outer series are almost always longer and narrower than the inner tepals. The outer tepals are apiculate. The apiculum frequently has a small, papillate horn on the adaxial surface in *Eucharis* subg. *Eucharis*. The inner tepals vary from acute to obtuse, sometimes minutely apiculate, at the apex.

The tepals of most species of subg. *Eucharis* spread at an angle of 90° or more from the throat. Perianth morphology of subg. *Eucharis* is thus predominantly crateriform. At times the tepals may be reflexed strongly above the midpoint of their length, or rarely for their entire length. Tepal habit varies even among flowers of the same inflorescence and shows no taxonomic consistency. If exposed to strong light, the abaxial midrib of the tepals of some species of subg. *Eucharis* may be lightly pigmented yellow.

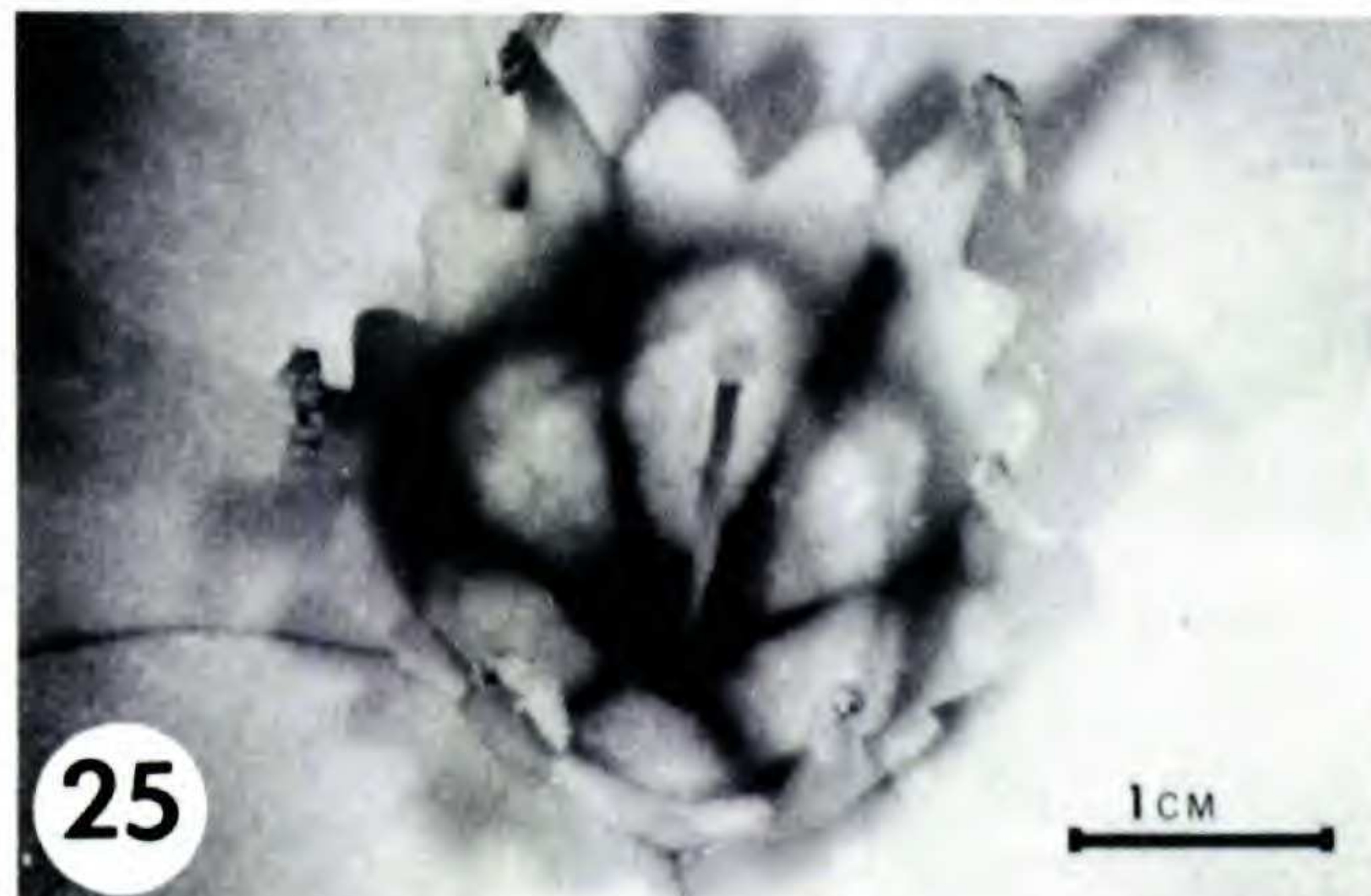
The perianth of *Caliphruria* is infundibular. The tepals remain imbricate for half their length and spread distally at angles of only 45 – 60° . The tepals of subg. *Heterocharis* are also for the most part imbricate proximally and spread at 45 – 60° from the throat. The perianth is more or less campan-

ulate. One species, *E. amazonica*, has the crateriform perianth characteristic of subg. *Eucharis* with a wide-spreading (ca. 90°) limb.

ANDROECIUM

The stamens of *Eucharis* and *Caliphruria* are variously connate proximally. In all but three species of *Eucharis*, a conspicuous staminal cup is present (Figs. 24, 25). In *Caliphruria*, the cup is reduced to a short, membranous, connate portion of the filaments near the perianth throat (Fig. 26). *Eucharis sanderi* (subg. *Heterocharis*) has a reduced staminal cup similar to that of *Caliphruria*. Staminal connation is one of the major characteristics of “infrafamily” Pancratioidinae. Some taxonomic workers considered the staminal cup of pancratioid genera homologous to the corona of *Narcissus* L. (e.g., Pax, 1888). The corona of *Narcissus* is generally considered to be of perianthal origin (Eichler, 1875; Arber, 1937), while the staminal cup of pancratioid taxa has been described as composed entirely of androecial tissue (Arber, 1937; Singh, 1972). Einsiedel (1987) and Müller-Doblies (pers. comm.) consider this distinction artificial and claim that both structures arise from the same meristematic potential, citing putative instances of polymorphy for both types within the same genus.

Stamens of *Eucharis* and *Caliphruria* may be dentate, edentate, or irregularly toothed. Both types of staminal morphology may occur in the same species, and variation may occur even among flow-



FIGURES 24–26. Androecial morphology of *Eucharis* and *Caliphruria* species.—24. *E. astrophiala* (Madison 3792, SEL).—25. *E. amazonica* (Schunke 14179, FLAS).—26. *C. subdentata* (Meerow 1109, FLAS).

ers of a single clone (Meerow, 1986). The presence or absence of staminal dentation has frequently been overweighted in the alpha-taxonomic literature relating to these genera (e.g., Ravenna, 1982) but can still be of taxonomic significance (e.g., *E. astrophiala* (Fig. 24), the only species of subg. *Eucharis* that always has an edentate staminal cup).

A variable pattern of green or yellow pigmentation is present in the androecium of all species of subg. *Eucharis* and *Heterocharis*. Stamens of *Caliphruria* are completely white. In subg. *Het-*

erocharis, the green (rarely yellowish) pigmentation is largely restricted to the interior of the cup, and extends into the dilated portion of the tube as well (Fig. 25). The coloration is concentrated along the filamental traces, but the tissue between the traces is also suffused with green. In subg. *Eucharis*, pigmentation is present on both the exterior and interior surfaces of the cup, does not extend into the dilated portion of the tube, and takes the form of either broad spots below each free filament or a uniform band of color at the basal $\frac{1}{2}$ – $\frac{1}{3}$ of the cup. In this subgenus, the pattern is of limited taxonomic significance. Whether the pigmentation functions as nectar guides for pollinating animals is unknown.

The stamens of most species of subg. *Eucharis* constrict distally into a broadly subulate portion (greater than 1 mm wide for most of its length) of varying length. Only in *E. astrophiala* (Fig. 24) and *E. bouchei* (in part) do the stamens constrict gradually from the rim of the staminal cup to the apex of the filament. The free filaments of *Caliphruria* are narrowly subulate (less than 1 mm wide for most of their length, Fig. 26). The free filaments of *E. sanderi* (subg. *Heterocharis*) are narrowly subulate and slightly incurved. Those of *E. moorei* and *E. amazonica* are broadly subulate.

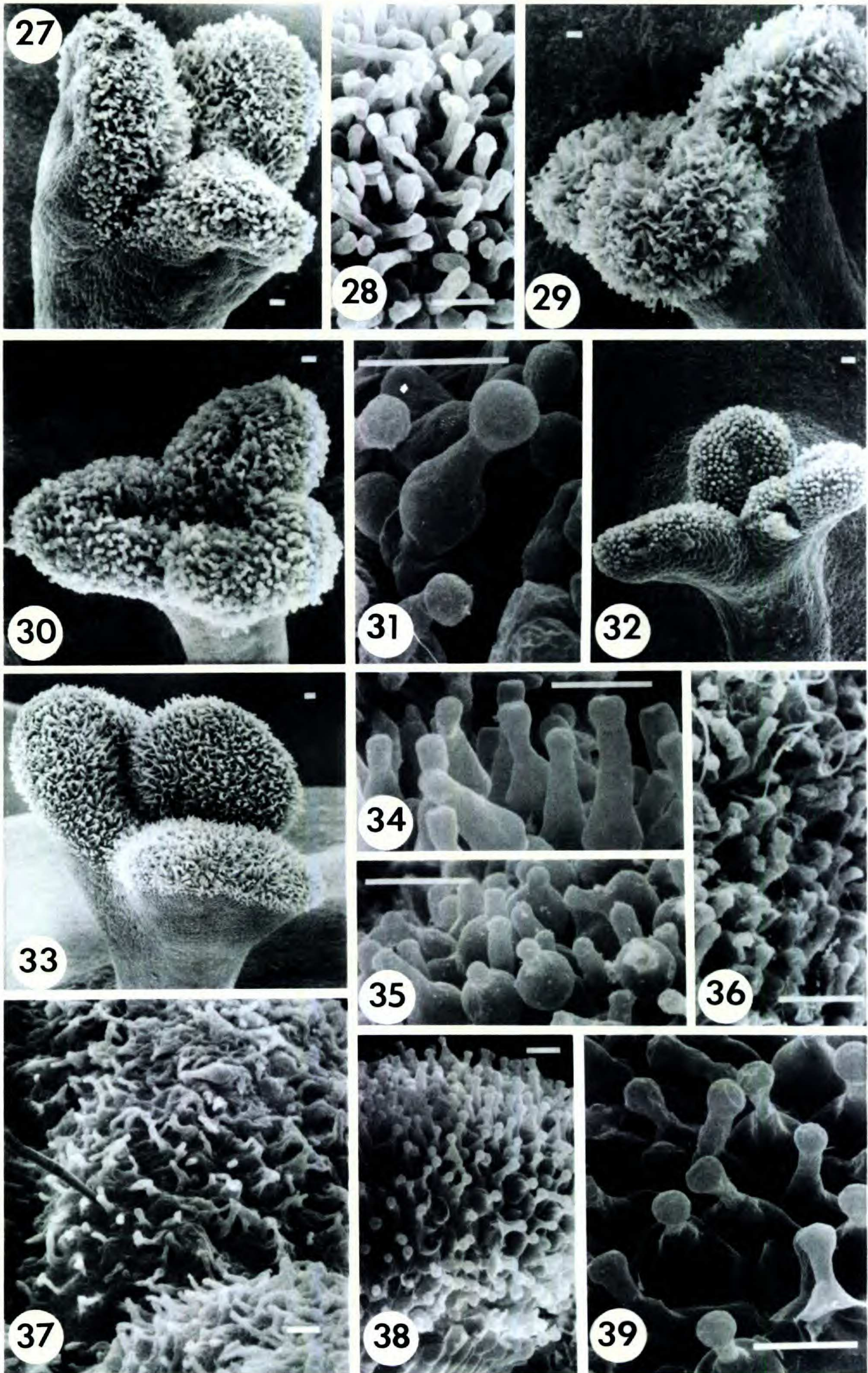
Anthers of *Eucharis* are introrse, dehiscing longitudinally, and either dorsifixed or sub-basifixed. They are most frequently oblong but are linear in subg. *Heterocharis*. At anthesis, the anthers of *Caliphruria* and *Eucharis* subg. *Eucharis* are erect but become versatile as they age. In subg. *Heterocharis*, the anthers are versatile at anthesis.

STIGMA AND STYLE

Of the sixteen species of *Eucharis* and *Caliphruria* observed in cultivation, all but *E. castelnaeana* are protandrous. Stigma receptivity does not occur until the second or third day following anther dehiscence. In some cases, the stigma does not fully expand until the perianth has begun to senesce. Successful greenhouse pollinations have been accomplished after the onset of perianth senescence. In the single known autogamous species, *E. castelnaeana*, stigma receptivity and anther dehiscence coincide.

The styles of *Eucharis* and *Caliphruria* are usually exerted beyond the anthers, most fre-

FIGURES 27–39. SEM photomicrographs of *Eucharis* and *Caliphruria* stigmas.—27, 28. *E. astrophiala* (Meerow 1111, FLAS).—29. *E. plicata* (Plowman 13941, FLAS).—30, 31. *C. subdentata* (Meerow 1152).—32. *C. korsakoffii* (Meerow 1096, FLAS).—33, 34. *E. × grandiflora* (Meerow 1127, FLAS).—35. *E. moorei* (Meerow



1141, FLAS).—36. *E. sanderi* (Cuatrecasas 16350, F).—37. *E. amazonica* (Schunke 14179, FLAS).—38, 39. × *Caliphruria butcheri* (Meerow 1110, FLAS). All scales = 50 μ m.



FIGURES 40-43. Fruits and seeds of *Eucharis* subg. *Eucharis*. 40, 41. Mature capsules.—40. *E. formosa* (Schunke 14174, FLAS).—41. *E. castelnaeana* (Schunke 14156, FLAS). 42, 43. Seeds.—42. *E. bouchei* var. *bouchei* (Meerow 1125, FLAS).—43. *E. castelnaeana* (Schunke 14156, FLAS).

quently 0.5–1 cm. In subg. *Heterocharis*, the styles are somewhat assurgent away from the stamens and are exerted well over 1 cm past the anthers. In two species of subg. *Eucharis*, *E. castelnaeana* and *E. plicata*, the style is included within the cup. In the former species, self-pollination occurs regularly, and stigma receptivity coincides with anthesis.

Stigmas of *Eucharis* and *Caliphruria* (Figs. 27, 29, 30, 32, 33) are obtusely trilobed. Trilobed stigmas are relatively rare in the Pancratioidinae, and *Urceolina*—sister group to *Eucharis* and *Caliphruria*—has a capitate, entire stigma. Traub (1963) and Traub & Moldenke (1949) considered a trilobed or trifid stigma the ancestral state in the Amaryllidaceae.

The stigmatic papillae of *Eucharis* are unicellular (Figs. 28, 34–37), while those of *Caliphruria* (Fig. 31) are multicellular, consisting of both a stalk cell and globose head cell. ×*Calicharis butcheri*, putatively a natural hybrid of *E. sanderi* and *C. subedentata*, has the multicellular stigmatic papillae (Figs. 38, 39) characteristic of *Caliphruria*. Heslop-Harrison & Shivanna (1977) characterized the stigmas of *Eucharis* and *Caliphruria* as dry-type.

OVARY AND OVULES

The ovary of *Eucharis* and *Caliphruria* is inferior and contains septal nectaries. It is green, with the exception of two species, *E. astrophiala* and *E. castelnaeana* (subg. *Eucharis*), in which the ovary is white at anthesis. Ovaries of *Eucharis* and *Caliphruria* range from oblong-ellipsoid (subg. *Heterocharis*) to globose or subglobose (*Caliphruria* and *Eucharis* subg. *Eucharis*). The ovary of subg. *Heterocharis* appears rostellate after senescence of the perianth.

The ovules of *Eucharis* and *Caliphruria* are globose, anatropous, and borne on axile placentae. Ovule number is quite variable throughout both genera. Within limits, however, this number is characteristic of species or species complexes. Subgenus *Heterocharis* has the largest ovule number in *Eucharis*, generally 16–20 per locule, but occasionally as low as 7 in *E. sanderi* (which otherwise has 16–20 throughout most of its range) and 9–12 in *E. amazonica*. In both *Caliphruria* and *Eucharis* subg. *Eucharis*, ovules do not number more than ten per locule. *Eucharis astrophiala*, *E. bouchei*, *E. bonplandii*, *E. cyaneosperma*, and *E. ulei* characteristically have two ovules per locule, but rarely as many as five.

FRUIT

The mature fruit of *Eucharis* and *Caliphruria* is a triloculicidal capsule typical of the nonbaccate-fruited Amaryllidaceae. In fruit, the pedicel elongates to two or more times its length at anthesis. In *Caliphruria* and *Eucharis* subg. *Heterocharis* (*E. moorei*), the capsule is thin-walled and green, sometimes turning yellow or brown at dehiscence. In subg. *Eucharis*, however, the capsule is leathery and bright orange (Fig. 40), contrasting vividly with the shiny black or blue seeds at dehiscence. It is probable, though unsubstantiated, that the combination of fruit and seed color functions mimetically to attract avian dispersal agents (sensu van der Pijl, 1982). In the single known exception to this characteristic fruit morphology in subg.

Eucharis, the fruit of *E. castelnaeana* (Fig. 41) remains green until shortly before dehiscence, at which time it yellows and finally turns brown. It is often tardily dehiscent and sometimes abscises before opening, though the seeds within are ripe.

SEED

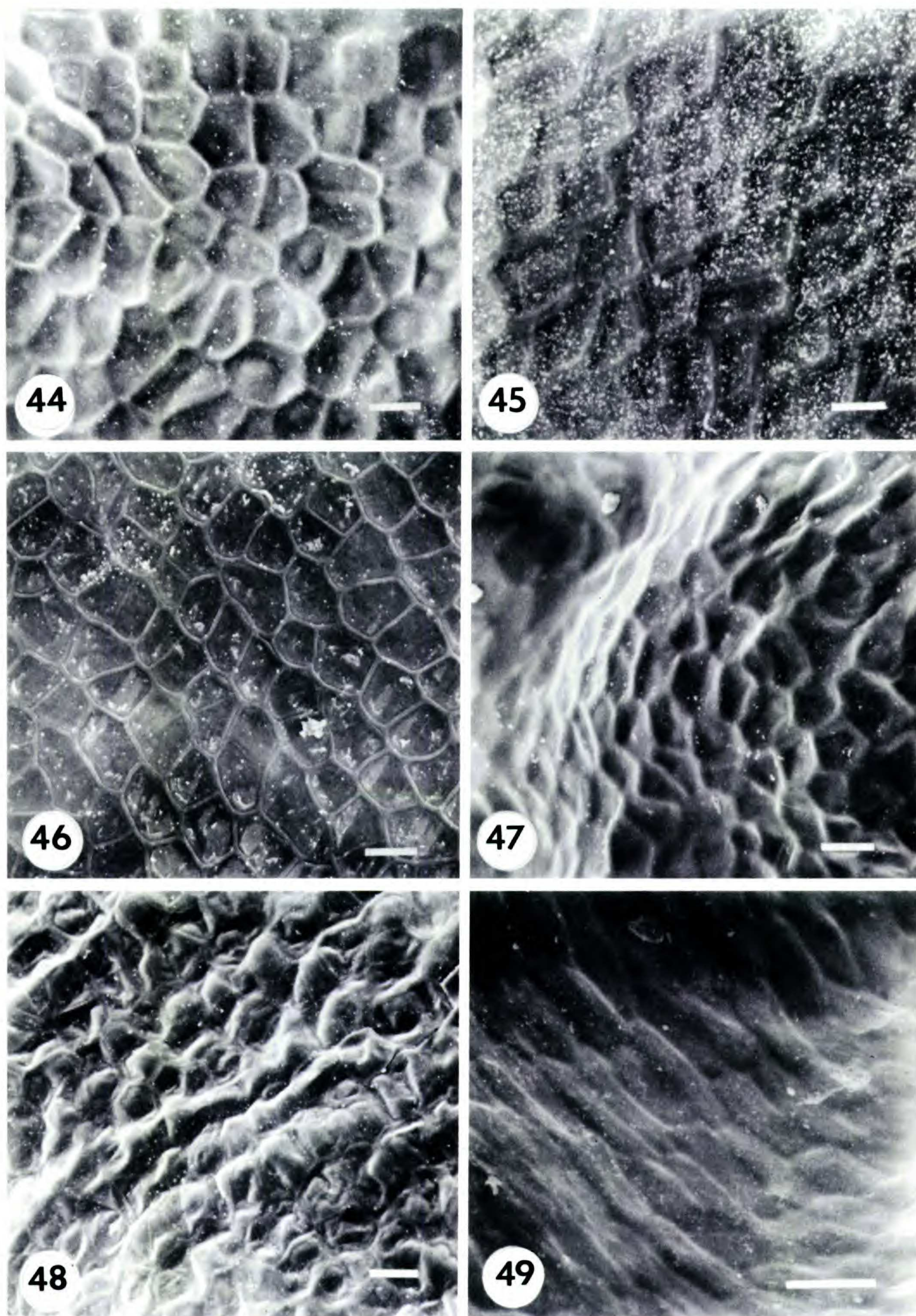
Regardless of the number of ovules per locule in any species of *Eucharis* and *Caliphruria*, all but a few abort as the fruit matures. Generally one to three seeds are present per locule in mature capsules, but as many as four have been observed (Fig. 40).

The seeds of both *Eucharis* and *Caliphruria* are globose or ellipsoid and turgid, the consequence of copious, oily endosperm and a high moisture content. Left at room temperature, the seeds will shrink away from the testa somewhat as moisture is lost but remain capable of germination. Long-term viability has not been tested.

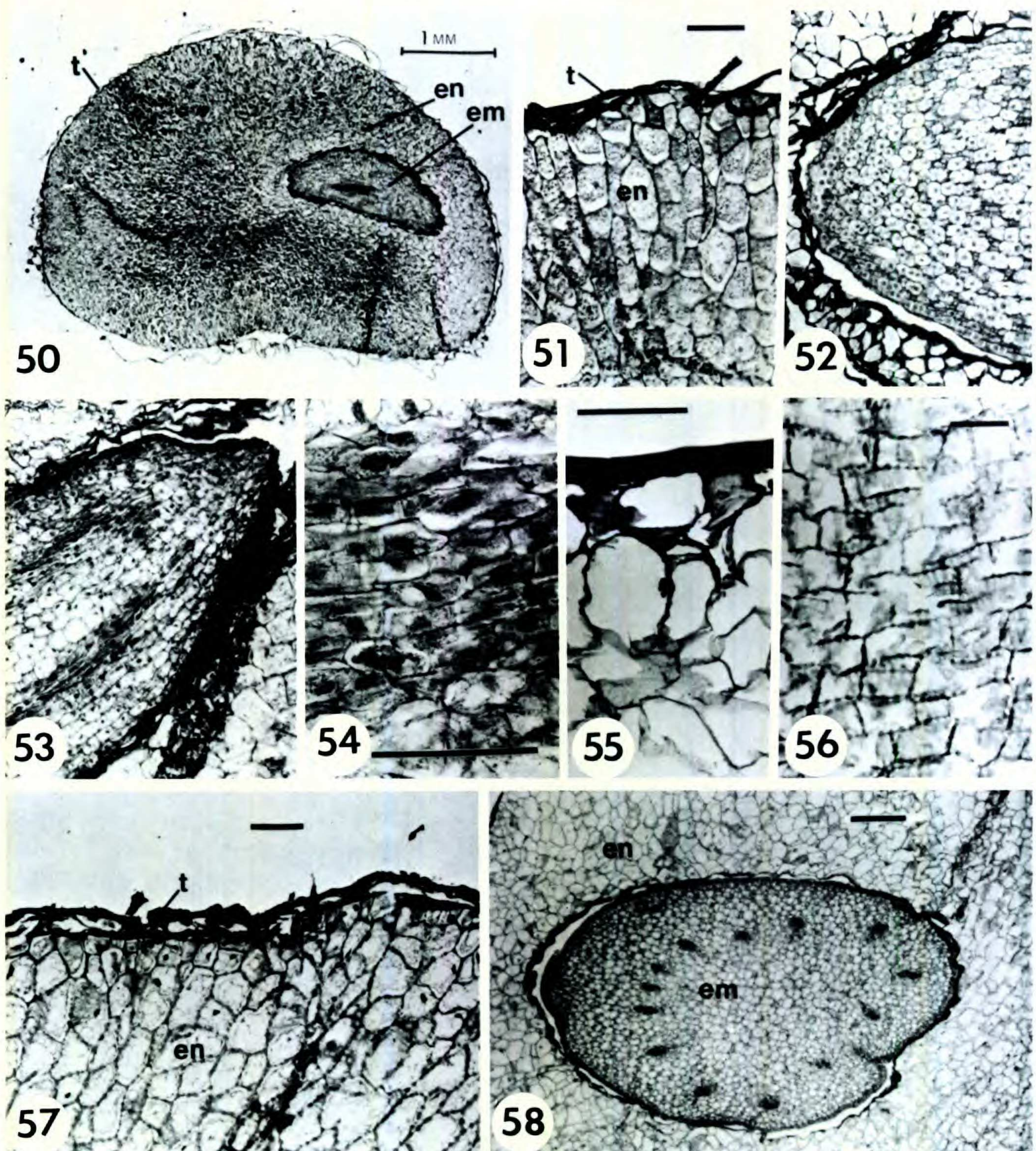
The seed of subg. *Eucharis* (Fig. 42) is characteristically ellipsoid and has a shiny, smooth black (blue in *E. cyaneosperma*) testa. The single exception so far known is again *E. castelnaeana* (Fig. 43). The seed of this species is wedge-shaped by compression in the capsule, is less turgid than seeds of consubgeneric species, and has a dull, rugose testa. The seed of *E. moorei* (subg. *Heterocharis*) is globose to very slightly compressed and has a brown, slightly rugose testa.

In *Caliphruria*, the seeds of only *C. korsakoffii* and *C. subedentata* are known. Seeds of *C. korsakoffii* are globose, turgid, and have a smooth, lustrous brown testa. Seed of *C. subedentata* is slightly compressed, with a lustrous black but rugose testa.

The testa is alveolate in all species examined (Figs. 44–49). In *E. bouchei* var. *dressleri* Meerow (Fig. 45), abundant wax extrusions are found across the surface. The testa of *Eucharis* and *Caliphruria* seeds is composed of phytomelan (Huber, 1969), a simple, largely inert, carbonaceous compound characteristically present in the seed coat of nonbaccate-fruited Amaryllidaceae (Dahlgren & Clifford, 1982; Huber, 1969). Werker & Fahn (1975) reported the occurrence of phenolic quinones in the phytomelan layer of *Pancratium* seeds. In most species of *Eucharis* and *Caliphruria*, the phytomelan layer is all that remains of the integuments (Figs. 51, 57). In *E. bouchei*, however, there is an additional layer of integument tissue about five cells thick, interposed between the phytomelan and the endosperm (Fig. 55). Whether this may be a consequence of the



FIGURES 44-49. SEM photomicrographs of *Eucharis* and *Caliphruria* seed surfaces.—44. *E. astrophiala* (Meerow 1111, FLAS).—45. *E. bouchei* var. *dressleri* (Meerow 1107, FLAS).—46. *E. formosa* (Meerow 1103).—47. *E. castelnaeana* (Schunke 14156, FLAS).—48. *C. korsakoffii* (Meerow 1096, FLAS).—49. *C. subdentata* (Meerow 1152, FLAS). All scales = 50 μm .



FIGURES 50-58. Photomicrographs of *Eucharis* and *Caliphruria* seed anatomy. 50-54. *C. korsakoffii* (Meerow 1096, FLAS).—50. Longitudinal section through whole seed.—51. Transverse section through testa and part of endosperm.—52. Longitudinal section through radicle of embryo.—53. Longitudinal section through apex of embryo.—54. Longitudinal section through vascular initial of embryo. 55, 56. *E. bouchei* var. *bouchei* (Meerow 1125, FLAS).—55. Transverse section through testa. Note several layers of additional integument cells below outer phytomelan layer.—56. Endosperm. Note transfer tissue with pitted walls and plasmodesmata. 57, 58. *E. castelnaeana* (Schunke 14156, FLAS).—57. Transverse section through testa and part of endosperm.—58. Transverse section through embryo. All scales = 100 μm except 40 μm in Figure 54. em = embryo, en = endosperm, t = testa.

tetraploid condition of this species is unknown. Most of the seed body of *Eucharis* and *Caliphruria* is taken up by a copious quantity of endosperm characterized by abundant transfer cells (Fig. 56). At maturity, no remnants of the nucellus were observed.

Most workers (e.g., Baker, 1888; Traub, 1963; Hutchinson, 1959; Dahlgren et al., 1985) have

allied *Eucharis* and *Caliphruria* with *Hymenocallis*, *Eurycles*, and *Calostemma* (e.g., tribe Eucharieae, or Eucharideae) on the basis of "fleshy seeds." The last-mentioned three genera do indeed have fleshy, bulbiform, sometimes viviparous seeds, but they are not homologous structures. The "pseudoseed" of *Eurycles* and *Calostemma* is actually an adventitious bulbil (Rendle, 1901). The bulbi-

form propagules of *Hymenocallis*, while true seeds, have thick, fleshy chlorenchymous integuments with a well-developed vascular system and a starch-storing embryo (Rendle, 1901; Whitehead & Brown, 1940). These important seed differences have been overlooked by most phylogenists of the Amaryllidaceae.

The turgid seed of *Eucharis* and *Caliphruria*, despite a high moisture content when first ripe, cannot be accurately described as fleshy. This becomes evident if the seed is allowed to dehydrate slightly at room temperature, and is most apparent in the hard seeds of *E. castelnaeana*, which, at capsule dehiscence, are less turgid than seeds of other species of subg. *Eucharis*. Seeds of *Eucharis* and *Caliphruria* have a reduced integument, represented in most cases only by the compressed phytomelan layer, and have never been observed to germinate viviparously. Phytomelan is absent from the testa of the pseudoseeds of *Eurycles* and *Calostemma*. It is present in only a single species of *Hymenocallis*, *H. quitoensis* Herbert (and probably its close relative *H. heliantha* Ravenna), which has been segregated into the separate genus *Lepidochiton* Sealy (1937) on this basis.

Seeds of *Pancratium* are structurally most similar to those of *Eucharis* and *Caliphruria*. Although variable in shape and surface features (Werker & Fahn, 1975), all species of *Pancratium* have a hard, turgid, ovoid or compressed seed body with copious endosperm (Meerow, unpubl. data; Werker & Fahn, 1975). All examined species of *Pancratium* have a phytomelanous and alveolate testa. Seeds of *Eucharis* and *Caliphruria* have a higher moisture content than those of *Pancratium*, all species of which occur in xeric to seasonally dry habitats.

POLLEN MORPHOLOGY

Pollen morphology of *Eucharis* and *Caliphruria* is reviewed in detail elsewhere (Meerow & Deghan, 1988) and will only be summarized here. Pollen grains of all species of *Eucharis* and *Caliphruria* (Figs. 59–62) are boat-shaped elliptic, monosulcate, heteropolar, and bilaterally symmetrical. The sulcus runs the length of the distal face of the grain. Exine sculpturing is semitectate/reticulate in all species examined.

Pollen of most *Eucharis* falls into Walker & Doyle's (1975) large size class (longest equatorial diameter 50–100 μm). A single species, *E. caucana*, has very large pollen (longest equatorial diameter as much as 110 μm). Pollen of *Eucharis* has average longest equatorial diameters greater

than 60 μm , with two exceptions: *E. castelnaeana* and *E. plicata* subsp. *brevidentata*, the two smallest-flowered species. Most species of *Eucharis* have pollen grains with longest equatorial diameters between 65 and 75 μm . Pollen of *Caliphruria* falls into the medium size class of Walker & Doyle (1975), with average longest equatorial diameters near 50 μm . Polar diameter of pollen of most *Eucharis* species ranges from 45 to 60.6 μm —diameters less than 40 μm are rare. Polar diameter of pollen of *Caliphruria* is always less than 40 μm . Exine reticulation of *Eucharis* is characteristically coarse (Figs. 59–61), while that of *Caliphruria* is fine (Fig. 62).

CHROMOSOME CYTOLOGY

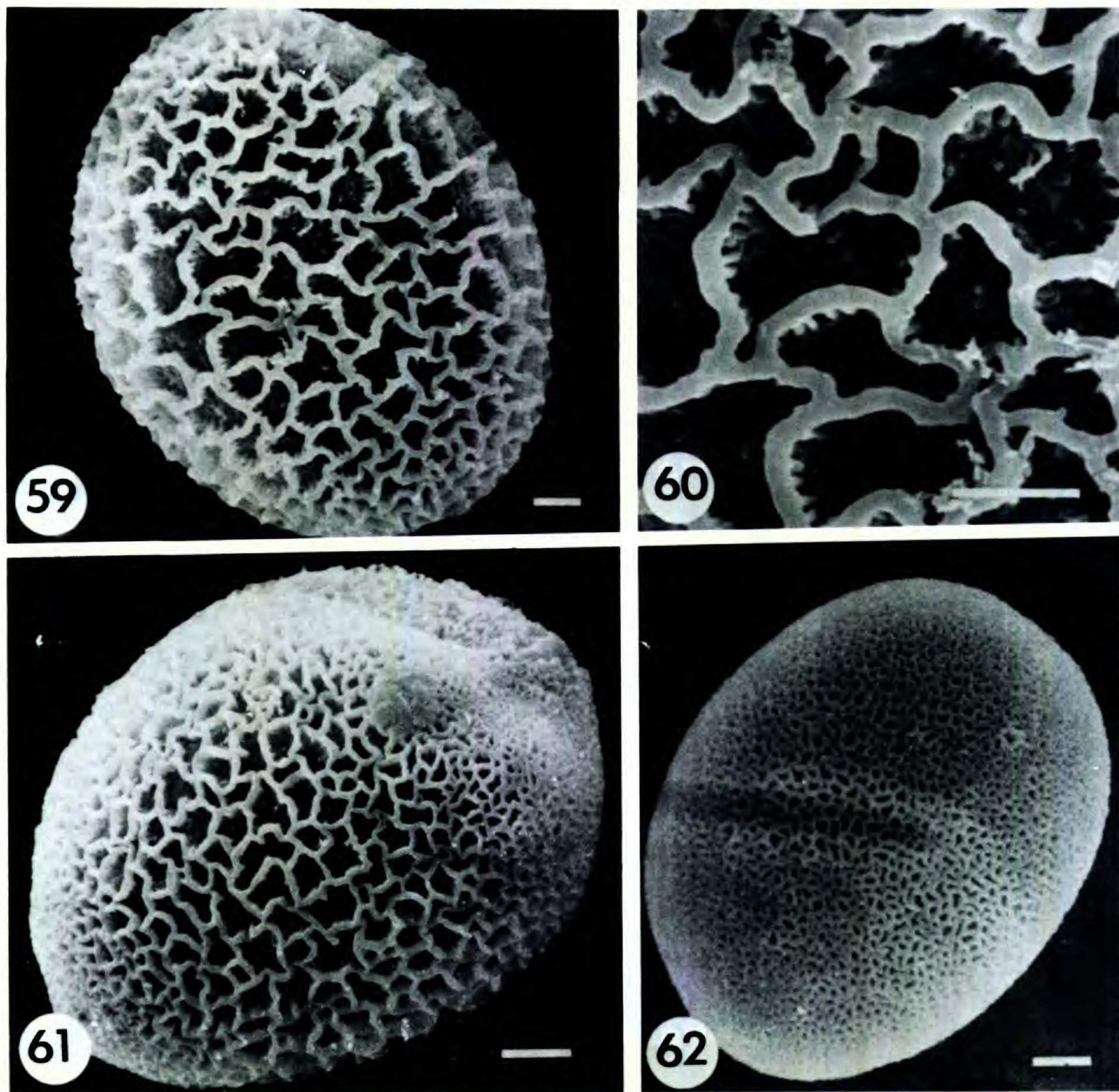
A somatic chromosome number of $2n = 46$ largely characterizes both genera (Meerow, 1987b). Two tetraploid species ($2n = 92$), *E. bonplandii* from Colombia and *E. bouchei* from Central America, are known. *Eucharis caucana*, described in this paper from Colombia, is a hexaploid with the largest chromosome number in the genus ($2n = 138$). *Eucharis amazonica*, $2n = 68$, is the only known departure from these $2x$, $4x$, or $6x$ karyotypes. A somatic chromosome number of $2n = 46$ (or derivations thereof) is characteristic of most genera of neotropical Pancratioidinae (Di Fulvio, 1973; Flory, 1977; Meerow, 1987b, c; Williams, 1981).

ECOLOGY AND PHYTOGEOGRAPHY

ECOLOGY

All species of *Eucharis* and *Caliphruria* exhibit high fidelity to a primary forest habitat, and severe disturbance of the forest canopy is catastrophic to the plants. In recently cleared forest sites, the bulbs persist for a few seasons, but the leaves developed in sunlight show chlorosis and necrosis. Wilkins (pers. comm.) reported that leaves of *E. amazonica* are damaged at light levels above 5,000 foot candles, an observation confirmed by Rees (1985). Fidelity of these genera to mesic, low-light habitats suggests a strongly evolved adaptive complex. Only two other genera of pancratioid Amaryllidaceae are completely adapted to forest understory: *Eurycles*, a small Australasian genus, and *Urceolina*, sister group to *Eucharis* and *Caliphruria*.

Eucharis populations are often largest on floodplains of small rivers and creeks where frequent short-term inundation is likely. *Eucharis* is also found in more upland sites, but usually in less abundance. No fully deciduous species of subg.



FIGURES 59–62. Representative pollen grains of *Eucharis* and *Caliphruria*. 59, 60. *E. formosa* (Meerow 1103, FLAS).—59. Whole grain, proximal polar view.—60. Detail of the exine surface.—61. *E. sanderi* (Killip 35401, US), oblique lateral longitudinal view.—62. *C. subedentata* (ex hort. s.n., K), proximal polar view. All scales = ca. 5 μm .

Eucharis have been observed, though *E. astrophia*, endemic to the western slopes of north-central Ecuador, enters a season of dormancy when growth ceases. Yet several leaves may persist for the duration.

The rarity of *Eucharis* and *Caliphruria* species throughout their range is a striking characteristic of their distribution. Single, widely dispersed clumps of bulbs are more the rule than the exception. Herbarium collections are usually unicates and often indicate the relative infrequency with which the plants were encountered in the forest. The largest population of *Eucharis* that I have observed consisted of about 30 individuals of *E. moorei* in an approximate half-hectare area. Throughout eastern Ecuador, populations of only two or three clonal clumps or single bulbs (and frequently as low as one) of *E. candida*, *E. formosa*, and *E. moorei* are common. In eastern Peru, a careful search

through a five-hectare area turned up only two plants of *E. cyaneosperma*. Edaphic conditions are probably important in limiting colonization and establishment of *Eucharis* species. Restriction to sites of high fertility is evident for all species of *Eucharis* and has been noted by floristic workers in the Amazon basin and Chocó region of Colombia (A. Gentry, pers. comm.).

No species of *Eucharis* are found natively above 1,800 m. The overwhelming majority of collections are from elevations below 1,000 m and, of these, more than half are below 500 m. *Caliphruria* is primarily collected at sites above 1,000 m (“selva-subandina” of Cuatrecasas, 1958). Most collections of *Caliphruria* (*C. subedentata*) were from the Río Cauca River valley of western Colombia, an area now largely deforested. In July 1984, I was not able to find members of this genus in any of its historical localities.

PHYTOGEOGRAPHY

More than half of the known species of *Eucharis* subg. *Eucharis* are found on the eastern slopes of the Andes. The majority of these species are concentrated along the Amazon and its main tributaries, e.g., the Napo and Pastaza system in Ecuador and the Huallaga of Peru. Seven of the fourteen extant species of subg. *Eucharis* are endemic to the premontane Andean–Amazonas interface, but no species has been reported east of 68°W longitude. Thus the genus appears to be absent from the great, largely Brazilian expanse of lowland Amazonas. Five peripheral isolate species from the premontane Andean–Amazonian center of distribution show some degree of morphological novelty (see Taxonomic Treatment). *Eucharis corynandra*, very closely related to *E. castelnaeana* and *E. plicata*, and *E. oxyandra*, of uncertain phylogenetic relationship, are both known only from the “ceja de la selva” forest formations of north-central eastern Peru. *Eucharis astrophiala* is endemic to a relatively small area of western Ecuador. *Eucharis lehmannii* and *E. caucana* are restricted to western Columbia. Of the five species, only *E. astrophiala* is known from other than the type locality.

Three of the four species of subg. *Eucharis* that occur above 2°N latitude are polyploids (chromosome number is unknown for *E. lehmannii*). *Eucharis bonplandii* ($2n = 92$), endemic to the Cordillera Oriental and Cordillera Central of Colombia is rare and infrequently collected. The *E. bouchei* complex ($2n = 92$), a series of geographically isolated and morphologically distinct population clusters (Meerow, 1987d), is endemic to Central America, chiefly Panama. *Eucharis caucana* is a hexaploid ($2n = 138$).

Subgenus *Heterocharis* is widely dispersed from Colombia to Peru, but each of its three species are narrowly distributed. With the exception of a single collection from northern Peru, *E. moorei* is not found outside of Ecuador. It is the only species of *Eucharis* found on both sides of the Andes. *Eucharis amazonica* occurs natively within a narrow area of the Río Huallaga valley in Peru. *Eucharis sanderi* is endemic to the Chocó region of Colombia.

Caliphruria is almost completely western Colombian, most prominently in the Río Cauca valley, with a secondary distribution in the Río Magdalena valley. *Caliphruria korsakoffii* is Peruvian.

ETHNOBOTANY

Labels of a number of herbarium specimens of *Eucharis* species indicate that lowland native peo-

ple collect the bulbs for use as poultices. The bulbs are mashed, heated, and applied to sores and tumors. Lewis (1986) described the use of mucilage from *Eucharis* bulbs (the plant illustrated is *E. formosa*) by the Jivaro Indians of Peru for treating facial blemishes and acne. Indian women of the Pastaza valley in Ecuador reportedly quite actively collect the plants in flower for reasons they would not disclose (N. Whitten, pers. comm.). Most local inhabitants whom I met while collecting *Eucharis* in the Oriente were readily familiar with the plants when shown photographs.

That various neotropical Amaryllidaceae have been cultivated in their native countries for many years cannot be discounted. Motifs recognizable as species of *Zephyranthes* Herbert and *Stenomesson* Herbert appear on ceremonial Incan vases (Vargas, 1981). The seasonal mass-blooming of *Hymenocallis amancaes* (Ruíz & Pavón) Nichols on the dry hills near Lima, Peru, has long been the nucleus of an annual festival named for that species (Herbert, 1839). I have suggested that frequent sympatric occurrence of *E. candida* and *E. formosa* in eastern Ecuador may have been influenced by cultivation by transient agriculturists (Meerow, 1987e). Further circumstantial evidence for this hypothesis is the persistence in nature of sterile hybrid taxa such as *E. × grandiflora* and *× Calicharis butcheri*. Almost all collections of the former are remnants of cultivation. *Eucharis oxyandra* is known only from bulbs found uprooted by an abandoned dwelling in Peruvian rain forest (see Taxonomic Treatment).

REPRODUCTIVE BIOLOGY

PHENOLOGY

Eucharis and *Caliphruria* species are largely seasonal flowering. Very well-collected species, such as *E. candida* or *E. formosa*, show flowering patterns skewed toward certain months (January to March), but at least several flowering collections have been made throughout the year. Species in Amazonian Peru have been collected in flower most frequently from June to September. Each inflorescence is moderately long-lived, two to three weeks, but usually no more than one to three flowers are open at any one time.

In the greenhouse, observations over a five-year period confirm an annual flowering for most *Eucharis* and *Caliphruria* species. *Eucharis amazonica*, however, flowers two or three times during the year. Van Bragt & Sprenkels (1983) have regularly induced flowering in this species at any time of the year after treatment at 27°C for at least two weeks. Collection data for this species

throughout its narrow range indicate that twice-annual phenology may occur in habitat as well. *Eucharis castelnaeana* mass-flowers in the greenhouse several times per year. Other well-collected species (e.g., *E. candida* and *E. formosa*) that show a peak period of flowering in certain months in nature are strictly annual-flowering in cultivation.

POLLINATION BIOLOGY

Data on pollination ecology of Amaryllidaceae in general are scant and represent an area sorely in need of investigation. No information on pollination of *Caliphruria* is available. The large, white, heavily and sweetly fragrant flower of *E. amazonica* (subg. *Heterocharis*) was considered a model moth-pollinated flower by Percival (1965). She noted that the nectar level in the tube rises to a maximum height of 23% tube length, thus effectively preventing access to all but long-tongued insects. The large, heavily fragrant flowers of subg. *Heterocharis* fit the syndrome of sphingid moth pollination (sensu Faegri & van der Pijl, 1979). Other related genera of "infrafamily" Pancratioidinae with similar flower morphology are specialized for hawkmoth pollination (*Hymenocallis*: Bauml, 1979; Grant, 1983; *Pancratium*: Morton, 1965).

Floral fragrance is rare in subg. *Eucharis*, occurring in only *E. bakeriana*, *E. castelnaeana*, *E. formosa*, and *E. plicata* subsp. *brevidentata*. However, floral fragrance is only weakly developed in these species, and in *E. formosa* the odor is slightly fetid. Vogel (1963) reported euglossine bees visiting *Eucharis bakeriana*. Visitation by an unidentified euglossine has been reported for other, unidentified species of subg. *Eucharis* in Peru (J. Schunke, pers. comm.). Unfortunately, neither report indicated the sex of the visitor. The phenology of *Eucharis* (rarely more than one or two flowers open per inflorescence at any one time over a period of two or three weeks, and the often successive appearance of inflorescences from a clonal clump of bulbs) and the dispersed distribution of plants in the wild suggests pollination by a trapping organism (see Janzen, 1971).

DISPERSAL

The leathery, bright orange fruit of *Eucharis* subg. *Eucharis* is a major apomorphy that defines the subgenus. At dehiscence, the contrast between the capsule and the lustrous black or blue seeds creates a striking visual display in the forest understory, but there are no recorded observations of visitation to the ripe capsules.

BREEDING SYSTEM

On the basis of greenhouse pollination attempts, virtually all species of *Eucharis* and *Caliphruria* demonstrate some degree of self-incompatibility. This observation suggests that most species are predominantly outcrossing. Capsules have been set readily with sibling pollen on all species in cultivation with the exception of *E. amazonica* and functionally sterile hybrid taxa (*E. × grandiflora*, *× Calicharis butcheri*). Further evidence of outcrossing is the marked protandry of most *Eucharis* species (with the exception of *E. castelnaeana*, in which stigma receptivity coincides with anthesis) and the presence of putative interspecific hybrids in nature (*E. candida* × *E. formosa* (Meerow, 1988), *E. plicata* subsp. *plicata* × *E. ulei* (Meerow, in prep.)). Of all species in cultivation, only *E. castelnaeana* sets capsules with self-pollen. Autogamy in *E. castelnaeana* is associated with a number of other divergent character states for subg. *Eucharis*. This species has a mass-flowering phenology; the smallest flowers in the genus; a green, often tardily dehiscent capsule; a less turgid seed with a dull, rugose testa; and telocentric chromosomes.

Reproductive biology of *Eucharis* and *Caliphruria* is thus still largely conjectural. Annual flowering patterns, short-term pollen viability, and susceptibility to systemic diseases in cultivation impede greenhouse exploration of these questions, and the rarity of the plants is an obstacle to field studies. The disappearance of populations of these genera and their pollinating agents, concurrent with rain forest destruction, may be the final impediment to investigation of this aspect of their biology.

PHYLOGENETIC RELATIONSHIPS

Eucharis and *Caliphruria* have been variously treated as separate genera (Baker, 1888; Bentham & Hooker, 1883; Pax, 1888; Hutchinson, 1959), a single genus (Traub, 1963), and as subgenera of *Urceolina* (Traub, 1971). As a group, *Eucharis*, *Caliphruria*, and *Urceolina* appear to represent a distinct tribal assemblage within "infrafamily" Pancratioidinae Traub (1957, 1963), a group delimited by various patterns of staminal connation, somatic chromosome number frequently of $2n = 46$, and an Andean center of diversity (Meerow, 1985, 1986, 1987a, c).

PHYLOGENETIC ANALYSIS

Despite a lack of consensus on generic and specific limits in Amaryllidaceae, cladistic analysis has only twice before been applied to such problems

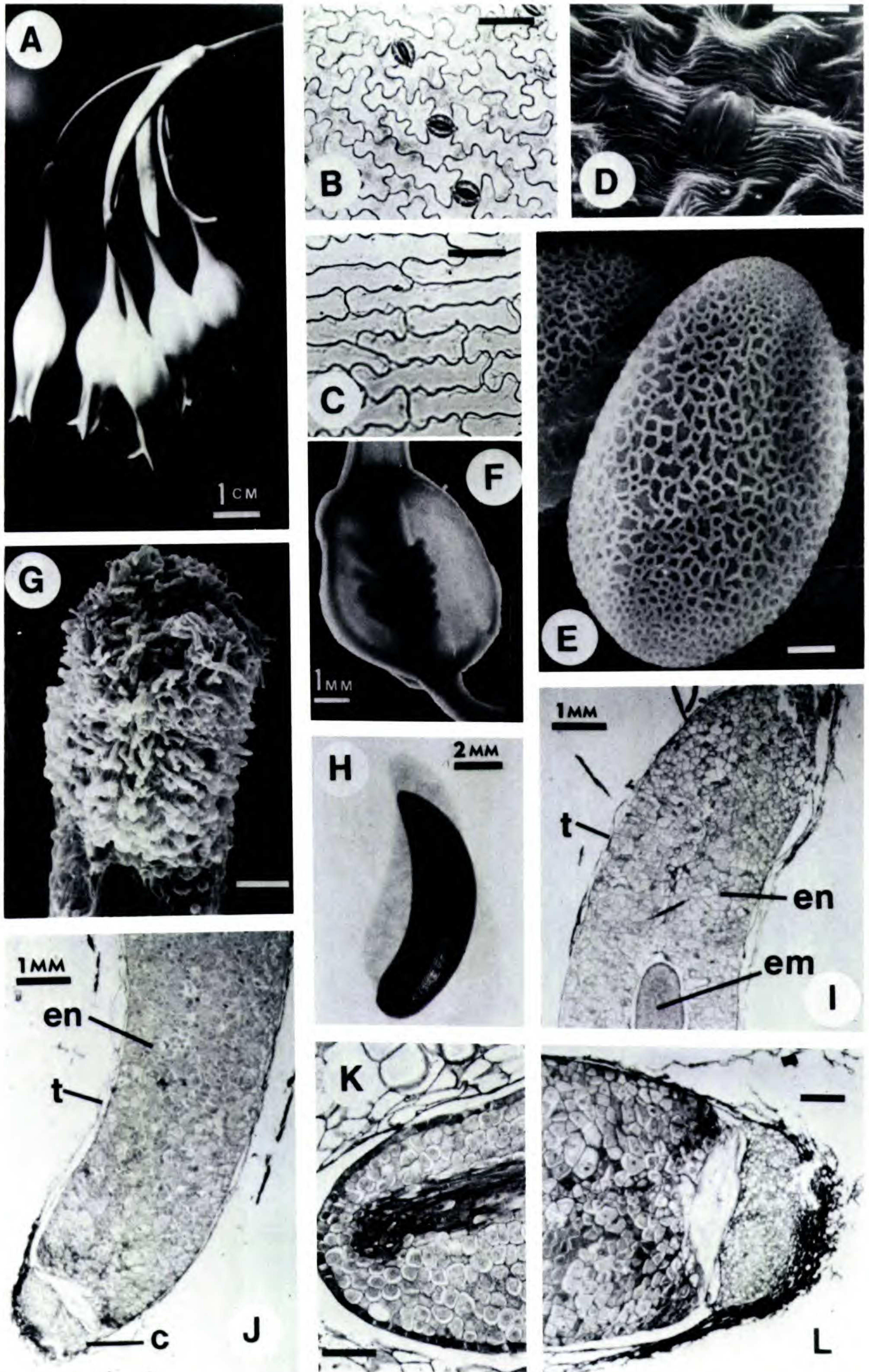


FIGURE 63. Character states of *Urceolina*. All photos are *U. microcrater* Kränz. (*Schunke 13633*, FLAS) unless otherwise stated. — A. Flowers (*Plowman & Kennedy 5721*, GH). Photo courtesy T. Plowman. B, C. Leaf epidermal cell configurations. — B. Abaxial surface. — C. Adaxial surface. — D. SEM photomicrograph of abaxial leaf surface. —

in the family, by Nordal & Duncan (1984) for *Haemanthus* L. and *Scadoxus* Raf., two closely related, baccate-fruited African genera; and Meerow (1987c) for *Eucrosia* Ker Gawler. The generic limits of *Eucharis* and *Caliphruria* in relation to *Urceolina*, as well as interspecific relationships in the former genera, seemed two areas that would benefit from the application of cladistic analysis. Before assessing these relationships cladistically, a brief review of character states in *Urceolina* is necessary.

Urceolina (ca. 6–8 species; Fig. 63) is so far known only from central and southern Peru on the eastern Andean slopes (Fig. 64) at elevations of 700–2,000 m. The relationships of *Urceolina* have long been misunderstood, most workers (Baker, 1888; Pax, 1888; Hutchinson, 1959) placing *Urceolina* near *Stenomesson* Herbert. Traub (1957) was the first to recognize its affinities with *Eucharis*. The problem no doubt stemmed from the inclusion of a species of *Stenomesson* (*S. miniatum* (Herbert) Ravenna) in *Urceolina* as *U. miniata* (Herbert) Benth. & Hook. Despite the ventricose aspect of the corolla morphology of *S. miniatum*, which is similar to that of *Urceolina*, the species clearly belongs to *Stenomesson* as evidenced by its narrow, subpetiolate leaves, the morphology of its staminal cup, and its numerous flat, black seeds (Ravenna, 1978).

Urceolina is easily distinguished by its brightly colored, urceolate corolla formed by the coherence of the tepals throughout most of their length (Fig. 63A). Vargas (1960) described the genus *Pseudourceolina* to accommodate a species of *Urceolina* in which the tepals are supposedly more laxly coherent. The morphology of the flower in *Urceolina* strongly suggests ornithophily (sensu Faegri & van der Pijl, 1979), i.e., vivid, “parrot” colors, ventricose corolla, pendulous habit, and absence of odor. As in *Caliphruria*, the staminal cup of *Urceolina* is reduced to a minute, membranous, basal connation of the filaments, which are otherwise linear throughout their length. The leaves of *Urceolina*, in thickness and lack of both surface plication and marginal undulation, resemble *Caliphruria* more closely than *Eucharis*. At least one species is hysteroanthous (*U. microcrater* Kränzlin), but all species enter a leafless dormant period in the wild. In size the pollen grains of *Urceolina* (Fig. 63E) are similar to those of *Caliphruria*. The

coarseness of the reticulum is intermediate between that of *Eucharis* and *Caliphruria*. In all species of *Urceolina* the small stigma is capitate and entire (Fig. 63G) versus the trilobed stigma found in *Eucharis* and *Caliphruria*. *Urceolina* species have 10–20 ovules. The ripe fruit of *Urceolina* is a thin-walled, yellow-green, turbinate capsule. The seeds of *U. microcrater* (Fig. 63H) are narrowly oblong, ca. 8 mm long, and 2.5 mm wide, and curved. The seeds have a unique anatomical feature: at the chalazal end, a dam of poorly differentiated tissue separates a “cap” composed of many small cells from the endosperm (Fig. 63J, L). The cells of the “cap” do not have pitted walls with plasmodesmata as is characteristic of the endosperm cells. There is no obvious surface feature on the seed corresponding to the area of this “cap,” and its function is unknown.

Outgroup selection. Preliminary cladistic analyses of the pancratioid Amaryllidaceae (Meerow, 1985) indicate that within the Pancratioidinae, a large, white, fragrant, crateriform flower with a conspicuous staminal cup (“pancratioid,” cf. *Pancratium* L.), involved with sphingid moth pollination (Bauml, 1979; Grant, 1983; Morton, 1965), may be symplesiomorphous. In other words, while the pancratioid flower was a major apomorphy defining the Pancratioidinae as a distinct group within the Amaryllidaceae, it is the ancestral floral morphology from which all other pancratioid taxa have diverged. I have used the term “the pancratioid base” to define the five genera of Pancratioidinae with this type of flower morphology (Meerow, 1985). These five genera are *Eucharis*, *Hymenocallis*, *Pancratium*, *Pamianthe* Stapf, and *Paramongaia* Velarde. All but *Pancratium* are entirely neotropical in distribution. The pancratioid flower correlates repeatedly with the largest pollen grain size within the Pancratioidinae (Meerow, 1985; Meerow & Dehgan, 1985). Putatively basal complexes within each pancratioid lineage also have numerous ovules per locule (ca. 20 or more), a character state considered primitive in the Amaryllidaceae (Traub, 1963).

Pollen morphology provides the best evidence for the monophyly of the Pancratioidinae. The large pollen grains of most species of the pancratioid base are uniformly coarsely reticulate, with some in each genus exhibiting a striking exine

←
E. SEM photomicrograph of *U. urceolata* pollen grain (*Weberbauer* 7822, US), proximal polar view.—F. Ovary.—G. SEM photomicrograph of stigma.—H. Seed. I–L. Longitudinal transverse sections of seed. em = embryo, en = endosperm, t = testa, c = cap.—I. Micropylar end of seed.—J. Chalazal end of seed.—K. Apex of embryo.—L. Internal chalazal “cap.” Scale bars B, C, G, K = 100 μ m; D = 25 μ m; E = 5 μ m; L = 200 μ m.

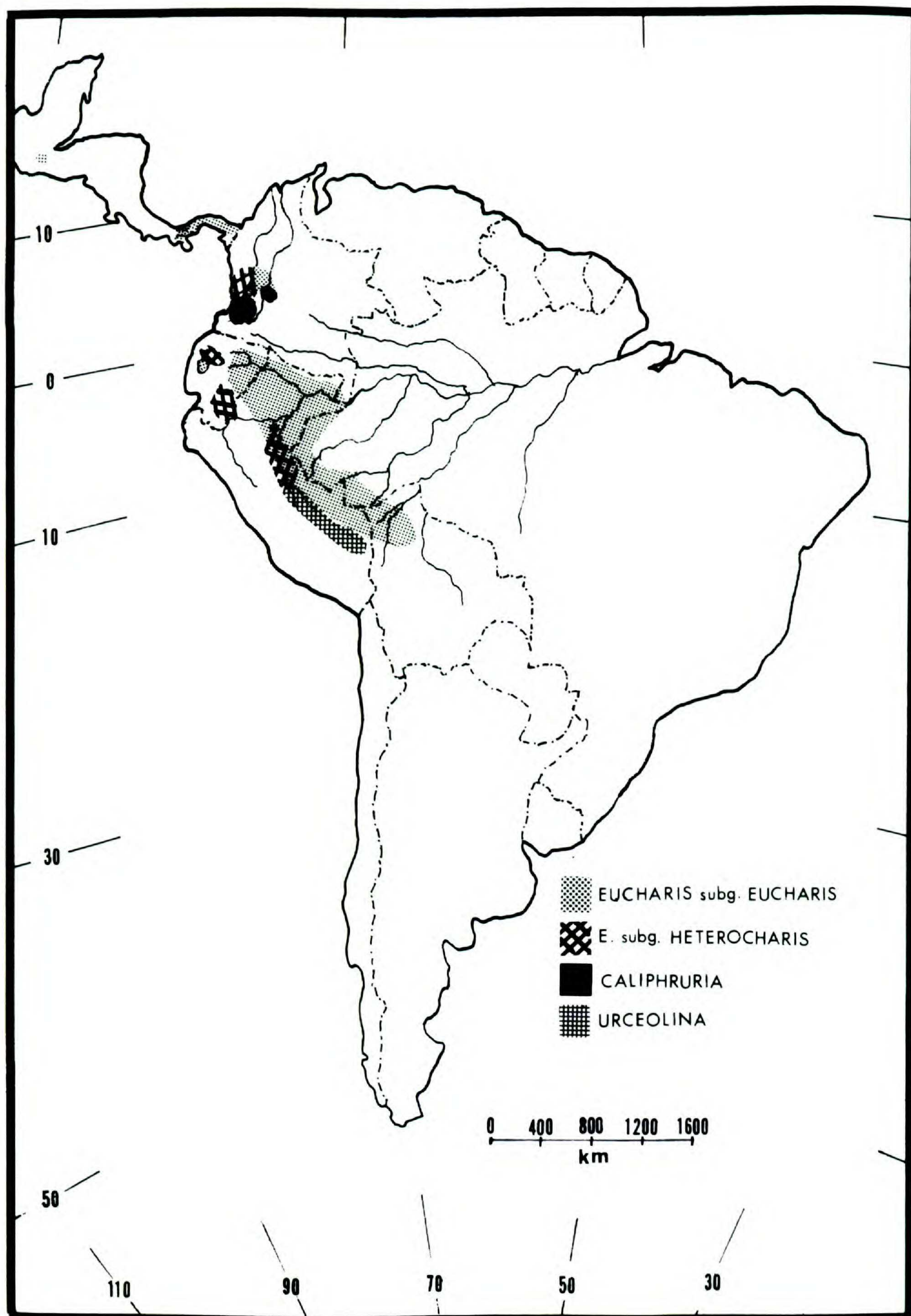


FIGURE 64. Generalized distributions of *Eucharis*, *Caliphruria*, and *Urceolina* in Central and South America.

dimorphism at the equatorial ends of the grain (Meerow, 1985; Meerow & Dehgan, 1985). Nonetheless, separate origins of the pancratioid flower in the Neo- and Paleotropics cannot be ruled out.

That the neotropical tribes of the Pancratioidinae represent a monophyletic group is a much more

robust hypothesis. All neotropical pancratioid genera have $2n = 46$ as the most common somatic chromosome number (Di Fulvio, 1973; Flory, 1977; Meerow, 1985, 1987a, c; Williams, 1981). This number may be derived from $2n = 22$, the most common somatic chromosome number in the family

TABLE 1. List of EUs and label designations for cladistic analysis of *Eucharis* and *Caliphruria*. * = outgroup.

Taxon	Designation
<i>Eucharis amazonica</i> Linden ex Planchon	AMA
<i>E. astrophiala</i> (Ravenna) Ravenna	AST
<i>E. bakeriana</i> N. E. Brown	BAK
<i>E. bonplandii</i> (Kunth) Traub	BON
<i>E. bouchei</i> Woodson & Allen	BOU
<i>E. candida</i> Planchon & Linden	CAN
<i>E. castelnaeana</i> (Baillon) Macbride	CAS
<i>E. caucana</i> Meerow	CAU
<i>E. corynandra</i> (Ravenna) Ravenna	COR
<i>E. cyaneosperma</i> Meerow	CYA
<i>E. formosa</i> Meerow	FOR
<i>E. lehmannii</i> Regel	LEH
<i>E. moorei</i> (Baker) Meerow	MOO
<i>E. oxyandra</i> (Ravenna) Ravenna	OXY
<i>E. plicata</i> subsp. <i>brevidentata</i> Meerow	PLI-B
<i>E. plicata</i> Meerow subsp. <i>plicata</i>	PLI-P
<i>E. sanderi</i> Baker	SAN
<i>E. ulei</i> Kränzlin	ULE
<i>Caliphruria hartwegiana</i> Herbert	HAR
<i>C. korsakoffii</i> (Traub) Meerow	KOR
<i>C. subdentata</i> Baker	SUB
<i>C. tenera</i> Baker	TEN
* <i>Pancratium</i> L.	PAN
<i>Urceolina</i> Reichb.	URC
<i>Lepidochiton</i> Sealy (<i>Hymenocallis quitoensis</i> & <i>H. heliantha</i>)	LEP

TABLE 2. Characters, character states, and transformation series for cladistic analysis of *Eucharis* and *Caliphruria*. * = unordered multistate character. A linear transformation series is implied for all ordered multistate characters except 41.

1. Leaves: 0, linear or lorate, sessile; 1, petiolate.
2*. Leaves: 0, deciduous; 1, deciduous and hysteranthous; 2, persistent.
3. Leaves: 0, plicate; 1, smooth.
4. Leaf margins: 0, nonundulate; 1, undulate.
5. Petiolar secondary bundles: 0, absent; 1, present.
6. Abaxial cuticular striations: 0, absent or nearly so; 1, dense, well developed.
7. Epidermal cell anticlinal walls: 0, more or less straight; 1, undulate.
8. Flowers: 0, more than 7 cm long; 1, 5–7 cm long; 2, less than 5 cm long.
9. Floral fragrance: 0, heavy; 1, mild; 2, absent.
10. Flower number: 0, more than 5; 1, ca. 5; 2, less than 5.
11*. Flower color: 0, white; 1, white or yellow; 2, yellow or orange.
12*. Flower habit: 0, erect or suberect; 1, declinate or pendent by curving of tube; 2, declinate or pendent by laxness of pedicel.
13. Pedicel length: 0, flower (sub)sessile; 1, less than 0.5 cm; 2, greater than 0.5 cm long.
14. Tube habit: 0, straight; 1, curved.
15. Tube length: 0, longer than tepals; 1, equal to or shorter than tepals.
16. Tube color: 0, green; 1, concolorous with tepals.
17*. Tube morphology: 0, cylindrical proximally, dilating at 1/2–1/3 of its length; 1, funnellform, dilating gradually from the base; 2, cylindrical for most of its length, dilating abruptly near the throat.
18*. Perianth morphology: 0, crateriform; 1, campanulate; 2, funnellform; 3, urecolate.
19. Staminal cup: 0, well developed; 1, reduced.
20. Androecial pigmentation: 0, present; 1, absent.
21. Staminal cup: 0, nonplicate; 1, plicate.
22. Staminal cup: 0, shallowly cleft between stamens (< 2 mm); 1, deeply cleft (> 2 mm).
23. Free filament: 0, linear (< 1 mm wide); 1, subulate (> 1 mm wide).
24. Staminal dentation: 0, present; 1, polymorphic; 2, absent.
25. Staminal teeth: 0, shorter than free filament; 1, more or less equal to free filament; 2, longer than free filament.
26. Anthers: 0, versatile at anthesis; 1, erect at anthesis.
27. Pollen longest equatorial diameter: 0, greater than 80 μm; 1, 76–80 μm; 2, 66–75 μm; 3, 60–65 μm; 4, 50–59 μm.
28. Pollen exine reticulation: 0, coarse; 1, moderately coarse; 2, fine.
29. Exine dimorphism: 0, present; 1, absent.
30. Style exerted: 0, greater than 1 cm beyond anthers; 1, 1 cm or less beyond anthers, but above the rim of the staminal cup; 2, to or below the rim of the staminal cup.
31. Stigma: 0, trilobed; 1, capitate, entire.
32. Stigmatic papillae: 0, unicellular; 1, multicellular.
33. Ovary color: 0, green; 1, white.
34. Ovary: 0, rostellate; 1, not rostellate.
35. Ovule number (per locule): 0, 10–20; 1, 7–10; 2, 3–6; 3, 2–3.
36. Ripe capsule: 0, green, relatively thin-walled; 1, leathery, thick-walled, orange.
37*. Seeds: 0, compressed; 1, globose or ellipsoid; 2, narrowly oblong, curved.
38*. Testa: 0, black; 1, blue; 2, brown.
39. Testa: 0, dull; 1, lustrous.
40. Testa: 0, smooth; 1, rugose.
41. Somatic chromosome number: A (00000), 22; B (10000), 34; C (01000), 46; D (01010), 68; E (01100), 92; F (01101), 138. A → B, A → C → D, C → E, E → F.

(Flory, 1977; Goldblatt, 1976; Meerow, 1984) via duplication or fragmentation of a chromosome, followed by doubling of the genome (Lakshmi, 1978; Sato, 1938). All paleotropical pancratioid genera have 22 or 20 chromosomes (Ponnamma, 1978; Zaman & Chakraborty, 1974).

Pancratium (ca. 17 species) and two species of *Hymenocallis* (*H. quitoensis* Herbert and *H. heliantha* Ravenna) were used as the primary outgroups in the analyses presented. Character state data on these taxa were accumulated from study of living material, herbarium specimens and literature (Björnstad, 1973; Meerow & Dehgan, 1985; Morton, 1965; Ponnamma, 1978; Ravenna, 1980; Traub, 1962; Werker & Fahn, 1975). *Pancratium* is putatively the least derived genus of the pancratioid base (Meerow, 1985). It is the only paleotropical genus of the group, and the only member with $2n = 22$ (Ponnamma, 1978), considered by most workers as the ancestral somatic chromosome number in the family (Flory, 1977; Goldblatt, 1976; Meerow, 1984).

The two species of *Hymenocallis* are undoubtedly a monophyletic group. They are the only two

TABLE 3. Character state matrix for cladistic analysis of *Eucharis* and *Caliphruria*. Refer to Table 1 for key to EU abbreviations, to Table 2 for characters. 9 = missing or inapplicable character state data. * = outgroup.

EU	Character																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
AMA	1	2	0	1	1	0	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0
MOO	1	2	0	1	1	0	0	0	0	1	0	1	1	1	0	0	0	2	0	0	0
SAN	1	2	1	1	0	1	1	0	0	2	0	1	1	1	0	0	0	2	1	0	9
AST	1	2	1	1	0	1	1	2	2	1	0	1	2	1	0	1	2	0	0	0	0
BAK	1	2	0	0	0	1	1	1	1	0	0	1	2	1	0	1	2	0	0	0	1
BON	1	2	0	0	0	1	1	1	2	1	0	1	2	1	0	1	2	0	0	0	0
BOU	1	2	0	0	0	0	1	1	2	1	0	1	1	1	0	1	2	0	0	0	0
CAN	1	2	1	1	0	1	1	1	2	0	0	1	2	1	0	1	2	0	0	0	0
CAS	1	2	1	1	0	1	1	2	1	0	0	1	2	1	0	1	2	0	0	0	1
CAU	1	2	1	1	0	1	1	1	2	2	0	1	1	1	0	1	0	1	1	0	9
COR	1	2	9	9	0	9	9	2	9	0	0	1	2	1	0	1	2	0	0	9	1
CYA	1	2	1	1	0	1	1	1	2	1	0	1	2	1	0	1	2	0	0	0	0
FOR	1	2	1	1	0	1	1	1	1	0	0	1	2	1	0	1	2	0	0	0	0
LEH	1	2	9	9	0	9	9	1	0	1	0	1	2	1	0	9	2	0	0	9	9
OXY	1	2	9	9	0	9	9	2	9	0	0	1	2	1	0	9	2	9	1	9	9
PLI-P	1	2	0	1	0	1	1	2	2	0	0	1	2	1	0	1	2	0	0	0	1
PLI-B	1	2	0	1	0	1	1	2	1	0	0	1	2	1	0	1	2	0	0	0	1
ULE	1	2	1	1	0	1	1	1	2	1	0	1	2	1	0	1	2	0	0	0	0
HAR	1	2	0	0	0	9	9	2	2	0	0	2	2	0	0	0	1	1	1	1	9
KOR	1	2	0	0	0	1	0	2	2	0	0	2	2	0	1	0	1	1	1	1	9
SUB	1	2	0	0	0	1	1	2	2	0	0	2	2	0	0	0	1	1	1	1	9
TEN	1	1	9	9	0	9	9	2	2	0	0	2	2	0	1	9	1	1	1	1	9
URC	1	1	0	0	0	1	1	1	2	0	2	2	2	0	0	1	2	3	1	1	9
LEP	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0
PAN*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

species of *Hymenocallis* with phytomelanous seed coats. All evidence suggests that possession of phytomelan is the ancestral condition in the Amaryllidaceae, and despite several independent losses, no reversal to the ancestral state has been proposed (Dahlgren & Clifford, 1982; Dahlgren & Rasmussen, 1983; Dahlgren et al., 1985; Huber, 1969). *Hymenocallis quitoensis* was segregated into a separate genus, *Lepidochiton* Sealy (1937) on the basis of phytomelanous seed. Both *H. quitoensis* and *H. heliantha* are ephemeral components of the xeric flora of southwestern Ecuador and northwestern Peru, and differ only in flower color. Traub (1962) considered *H. quitoensis* a relict and the most primitive species of *Hymenocallis* on the basis of ovule number (ca. 20 per locule; 2–10 occurs in all other species) and chromosome number ($2n = 24$, based on Snoad, 1952); however, collections from Peru and Ecuador that I have examined have $2n = 34$. These are the lowest reported chromosome numbers in the genus (Flory, 1976). These species will be called *Lepidochiton* in the following discussion. Additional analyses were run using other members of the

pancratioid base as outgroups (*Hymenocallis* subg. *Hymenocallis*, *H.* subg. *Ismene* (Salisb.) Baker ex Traub, *Pamianthe*, and *Paramongaia*). The resulting cladograms were either equal in length or slightly less parsimonious than those presented here; they did not show changes in the resolution of terminal taxa from the cladograms presented.

Ordered characters. Ten of the 18 multistate characters (Table 2) used in these analyses (8, 9, 10, 13, 24, 25, 27, 28, 30, and 35) were ordered into linear transformation series. Study of character state correlations among all genera of the pancratioid Amaryllidaceae (Meerow, 1985, 1987a, c) strongly suggests that flower size reduction (8), loss of floral fragrance (9), flower number (10), pedicel length (13), staminal tooth length (25), style length (30), and reduction in ovule number (35) have evolved in this stepwise manner with no evidence of reversal. Numerous ovules per locule (20 or more) characterizes all basal genera of the pancratioid Amaryllidaceae and is generally considered the ancestral condition for the family (Traub, 1962, 1963; Traub & Moldenke, 1949). Though the

TABLE 3. Continued.

Character																			
22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	9	0	9	9	01010
0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	2	0	1	01000
9	0	2	9	0	3	0	0	0	0	0	0	0	0	9	9	9	9	9	99999
1	1	2	9	1	0	0	1	1	0	0	1	1	3	1	1	0	1	0	01000
0	1	0	0	1	1	0	1	1	0	0	0	1	1	1	1	0	1	0	01000
1	1	0	0	1	3	0	1	1	0	0	0	1	3	1	1	0	1	0	01100
1	1	1	1	1	2	0	1	0	0	0	0	1	3	1	1	0	1	0	01100
1	1	1	0	1	2	0	1	1	0	0	0	1	2	1	1	0	1	0	01000
0	1	0	0	1	4	0	1	2	0	0	1	1	2	0	0	0	0	1	01000
9	1	2	9	1	0	0	1	1	0	0	0	1	2	1	1	0	1	0	01011
0	1	0	0	1	9	0	1	1	0	0	9	1	2	9	9	9	9	9	99999
1	1	1	0	1	2	0	1	1	0	0	0	1	3	1	1	1	1	0	01000
1	1	1	0	1	2	0	1	1	0	0	0	1	1	1	1	0	1	0	01000
1	0	0	1	1	9	9	9	1	0	0	9	9	1	9	9	9	9	9	99999
9	0	1	0	1	2	1	0	1	0	0	9	1	1	9	9	9	9	9	99999
0	1	0	2	1	2	0	1	2	0	0	0	1	1	1	1	0	1	0	01000
0	1	0	1	1	3	0	1	2	0	0	0	1	2	1	1	0	1	0	01000
1	1	1	0	1	2	0	1	1	0	0	0	1	3	1	1	0	1	0	01000
9	0	0	1	1	4	2	1	1	0	1	0	1	3	0	9	9	9	9	99999
9	0	2	9	1	4	1	0	1	0	1	0	1	2	0	1	2	0	0	01000
9	0	2	9	1	4	2	1	1	0	1	0	1	2	0	0	0	0	1	01000
9	0	0	2	1	4	2	1	1	0	1	0	1	3	0	9	9	9	9	99999
9	0	0	0	0	4	1	0	0	1	0	0	1	0	0	2	0	1	0	01000
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	0	0	10000
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	00000

evidence from phenetic studies of *Eucharis* (Meerow, 1987d, in press) and from study of other genera of the pancratioid Amaryllidaceae (e.g., Meerow, 1987c) indicates that androecial characters are among the most plastic morphological characters in this group, examination of the evolutionary patterns of staminal dentation (24) within various genera (Meerow, 1987c, in press) suggests that a reversal to the dentate state is unlikely once dentation is lost completely. Complete loss of staminal dentation often accompanies overall phenetic divergence among the pancratioid genera (Meerow, 1985, 1987c; see *E. astrophiala* in this paper). Polymorphism for the character is not uncommon, however, and is conceived in the transformation series as the intermediate between the two fixed states of toothed or edentate stamens. Ordering of pollen size (27) and exine morphology (28) is based on data presented in Meerow (1985, 1987c) and Meerow & Dehgan (1985), as well as unpublished palynological data accumulated for many genera in the family. A single character, chromosome number (41), was coded in additive binary on the basis of much literature on amaryllid cytology (Flory, 1976, 1977; Goldblatt, 1976; Lakshmi, 1978;

Meerow, 1984, 1987b; Ponnamma, 1978; Sato, 1938; Snoad, 1952), which strongly supports this concept of chromosome number evolution.

Results and discussion. Twelve most parsimonious trees without any differences in topology resulted when either *Pancratium* or *Lepidochiton* was used as the outgroup. The twelve trees differed only in the branch lengths of a few internal nodes, and resolution of terminal taxa did not change among them. One of the twelve with *Pancratium* used as outgroup is illustrated and discussed in detail (Fig. 65). The cladogram has a length of 92.4 steps (fractional lengths are a result of weight scaling), and a consistency index (CI; Kluge & Farris, 1969) of 0.487. *Lepidochiton* is the first terminal EU to resolve in the cladogram after the outgroup, *Pancratium*. Character state changes from the outgroup to the ancestral node of *Lepidochiton* (flower number reduction, globose seeds) could not be polarized. Uniflory, perianth color polymorphism, brown seed testa, and $2n = 34$ are the four apomorphies of *Lepidochiton*. The next internal node of the cladogram is the hypothetical ancestor to *Eucharis*, *Caliphruria*, and *Urceolina*,

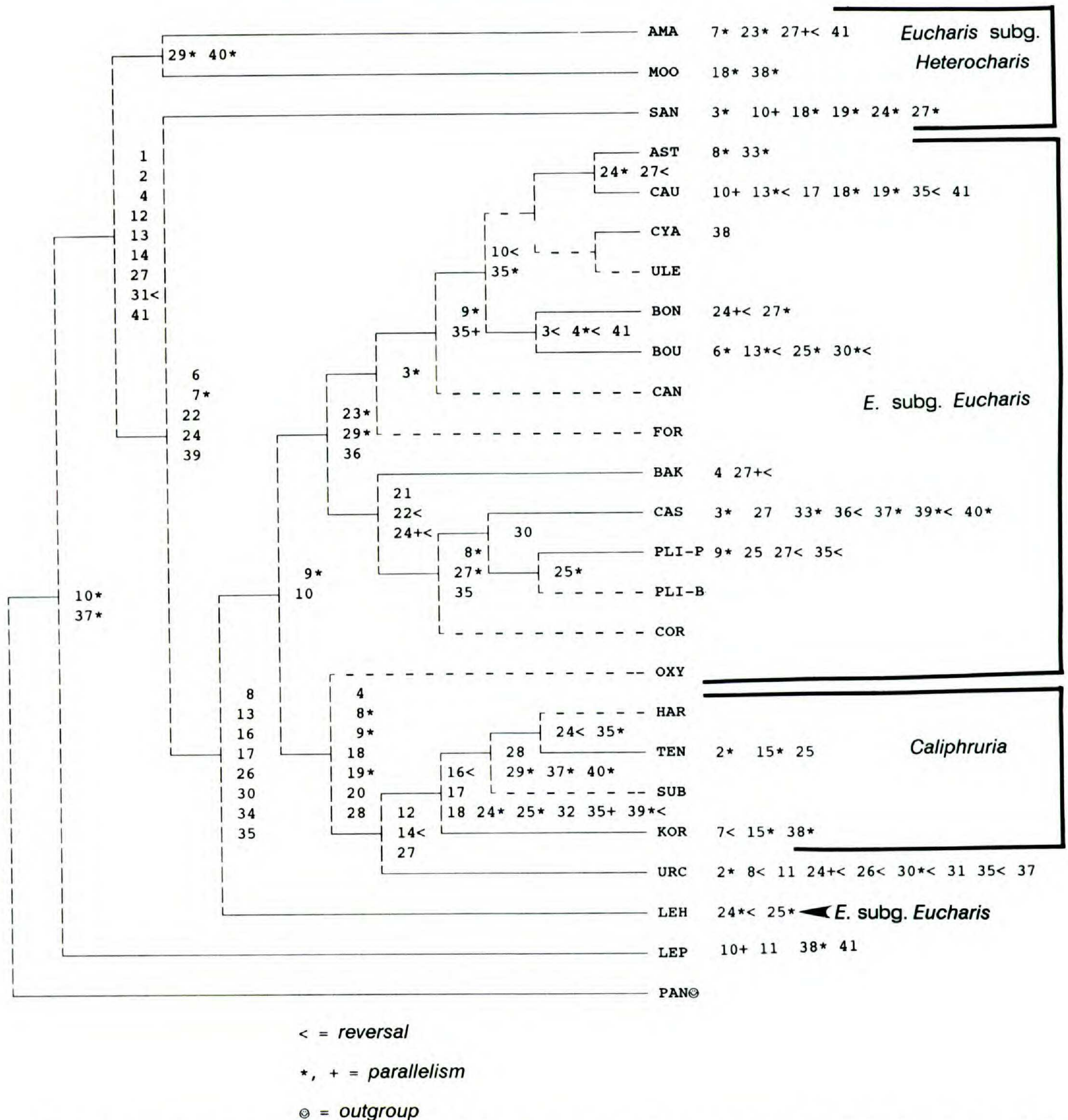


FIGURE 65. Cladogram of *Eucharis* and *Caliphruria*, based on data matrix in Table 3. Broken horizontal line indicates zero-length branch. Numbers inside refer to apomorphies of adjacent EU or internal node. Refer to Table 1 for EU designations.

all of which thus form a monophyletic group. Nine apomorphies occur at this node. The most important are the evolution and fixation of the evergreen, petiolate leaf; the changes in flower habit, pedicel length, tube morphology, and pollen size; trilobed stigmas; and increased chromosome number.

The rest of the cladogram forms two monophyletic groups. The smaller group represents part of my concept of subg. *Heterocharis*, *E. amazonica* and *E. moorei*, linked by three apomorphies: secondary petiolar bundles, loss of pollen exine dimorphism, and rugose testa (the state for the last-mentioned character is unknown for *E. ama-*

zonica). The larger monophyletic group represents *E. sanderi*, *Eucharis* subg. *Eucharis*, *Caliphruria*, and *Urceolina*. Five apomorphies define the ancestral node: densely striate abaxial cuticle, undulate anticlinal walls (homoplasious with *E. amazonica*), deeply cleft staminal cup, polymorphism in staminal dentation, and lustrous testa. It is thus obvious that subg. *Heterocharis* is paraphyletic according to this cladogram. *Eucharis moorei* and *E. amazonica* also resolve cladistically as the most basal species of *Eucharis*.

Eucharis sanderi is cladistically basal to the remaining EUs with which it forms a monophyletic

group. The six apomorphies of *E. sanderi* are plicate leaves, reduction in flower number, campanulate perianth (homoplasious with *E. moorei*), reduced staminal cup, loss of staminal dentation, and yet further reduced pollen grain size.

The next monophyletic group is supported by eight apomorphies and comprises *Eucharis* subg. *Eucharis*, *Caliphruria*, and *Urceolina*. Apomorphies at the ancestral node are reduced flower size, increased pedicel length, loss of green tube pigmentation, change in tube dilation, erect anthers, decreased style exertion, nonrostellate ovary, and decreased ovule number. *Eucharis lehmannii* is cladistically basal to the remaining EUs in the cladogram and is defined by two apomorphies: a reversal to dentate stamens and an increase in the length of the teeth. The remainder of the cladogram forms two monophyletic groups. All but two species of *Eucharis* subg. *Eucharis* comprise one, and *Caliphruria*, *Urceolina*, and *E. oxyandra* constitute the second. Only two apomorphies define this clade: reduction in floral fragrance and an increase in flower number.

The three apomorphies at the ancestral node of the *Eucharis* subg. *Eucharis* clade are subulate free filaments (homoplasious with *E. amazonica*), loss of exine dimorphism (homoplasious with the ancestor of *E. amazonica* and *E. moorei*), and an orange capsule. Within this clade, two monophyletic groups are evident. The larger of the two is defined by a single apomorphy, plicate leaves. *Eucharis formosa* is the first terminal EU to resolve but terminates a zero-length branch. *Eucharis candida* also terminates a zero-length branch, the ancestral node of which is defined by two apomorphies: loss of floral fragrance and reduction in ovule number. The next monophyletic group encompasses all species of subg. *Eucharis* with about five flowers and about two ovules per locule. The hypothetical ancestor of *Eucharis astrophiala* and *E. caucana* forms an unresolved polytomy at the ancestral node with *E. cyaneosperma*, *E. ulei*, and the hypothetical ancestor of tetraploid species *E. bonplandii* and *E. bouchei*.

Three apomorphies define the ancestral node of the second clade within subg. *Eucharis*: a plicate staminal cup, a reversal to shallowly cleft staminal cups, and a reversal from polymorphism in staminal dentation to fixed dentation. *Eucharis bakeriana* is the first terminal EU to resolve, on the basis of two apomorphies: loss of leaf margin undulation and increase in pollen size. The remaining species are the smallest-flowered species in the subgenus. The remaining apomorphies at the ancestral node are a decrease in pollen size and ovule number.

The first terminal EU to resolve is *E. corynandra*, from a zero-length branch. It should be noted, however, that two autapomorphies of this species, a short staminal cup and club-shaped free filaments, were not included in the data matrix. The ancestor of the two subspecies of *E. plicata* form a monophyletic group with *E. castelnaeana* on the basis of style length. Subspecies *brevidentata* terminates a zero-length branch. *Eucharis castelnaeana* has the greatest patristic distance of the three EUs (seven apomorphies).

The final large clade constitutes *Caliphruria*, *Urceolina*, and the cladistically basal *E. oxyandra*. Apomorphies are nonundulate leaf margins, small flowers, loss of floral fragrance, urceolate corolla (which does not apply to *E. oxyandra*, the corolla shape of which is either crateriform or campanulate but could not be coded as one or the other with certainty), reduction of the staminal cup, loss of androecial pigmentation, and moderately coarse exine. The character state of *E. oxyandra* is unknown for four of these seven. Within this monophyletic group, *Urceolina* and the hypothetical ancestor of *Caliphruria* resolve as sister groups on the basis of three apomorphies: declinate or pendent flowers via pedicel habit, straight tubes, and small pollen grains. Nine and eight apomorphies define *Urceolina* and the hypothetical ancestor of *Caliphruria*, respectively. Within *Caliphruria*, the sole representative of the genus outside Colombia, *C. korsakoffii* is the first terminal EU to resolve, on the basis of three apomorphies: straight anticlinal epidermal walls, short tubes (homoplasious with *C. tenera*), and brown testa. *Caliphruria subedentata* terminates a zero-length branch from the hypothetical ancestor of the Colombian species of the genus. Apomorphies at the ancestral node are finely reticulate exines, loss of exine dimorphism, compressed seeds, and rugose testa (the states for the last two characters are known only for *C. subedentata*). *Caliphruria hartwegiana* and *C. tenera* form a monophyletic group on the basis of toothed stamens and reduced ovule number, but *C. hartwegiana* terminates a zero-length branch.

The cladogram presented in Figure 65 contains 70 parallel origins of character states and 29 reversals (unordered characters not included). This may raise questions concerning the homology of characters that manifest low consistency. If the data matrix is analyzed with all characters removed that exhibit three or more independent origins for the same state (characters 3, 4, 8, 9, 10, 18, 19, 24, 25, 27, 29, 35, 37, 38, 40), the three trees that result have a fourfold increase in zero-length

branches and unresolved polytomies. Invariably, it is androecial characters (including pollen size) in which a great deal of homoplasy has occurred. Three of all the androecial characters, 24 (staminal dentation), 25 (length of teeth), and 27 (pollen size), are particularly homoplasious. When the data matrix was run with only these characters deleted, no change occurred in the resolution of terminal taxa from the cladogram in Figure 65. Finally, the data matrix was analyzed with all staminal cup characters (19, 20, 21, 22, 23, 24, 25), and pollen size (27) deleted. The resulting three cladograms (differing only by one internal branch length) placed *Caliphruria* and *Urceolina* within a monophyletic group including *E. bakeriana*, *E. bonplandii*, and *E. bouchei*, on the basis of a single apomorphy, nonundulate leaf margins.

Regardless of how the character-state data are manipulated, a number of monophyletic groups appear particularly robust. That *Eucharis*, *Caliphruria*, and *Urceolina* represent a monophyletic group is uncontested. The monophyly of *Eucharis moorei* and *E. amazonica* is also strongly supported, and these two species are the most cladistically basal of the eucharoid lineage. These species have the greatest number of putatively primitive characters and seem to represent the more ancestral species in the genus. Nonetheless, according to the cladogram in Figure 65, retaining subg. *Heterocharis* in *Eucharis* renders the genus paraphyletic. Subgenus *Heterocharis* is a fairly heterogeneous group from the perspective of apomorphic characters alone. Each of the three species may be characterized by autapomorphies, but only plesiomorphies join them. By including subg. *Heterocharis* in *Eucharis*, *Eucharis* becomes paraphyletic according to this cladogram. However, it should be noted that it is unknown whether secondary petiolar bundles (which require fresh material to observe), an important apomorphy which links *E. amazonica* and *E. moorei*, are present in *E. sanderi*. In the generalized sense, the distribution of subg. *Heterocharis* is quite broad, from Colombia to Peru (Fig. 64). However, each of the three species of subg. *Heterocharis* itself are only narrowly distributed. *Eucharis sanderi* is known only from the Chocó region of Colombia. *Eucharis amazonica* is found natively only in the middle Río Huallaga valley of Peru. *Eucharis moorei* has been collected outside of Ecuador only once. More significantly, *E. moorei* is the only species of *Eucharis* found on both sides of the Andes. I believe that all three species of subg. *Heterocharis* represent the relictual remnants of the ancestral eucharoid complex, each of which has remained iso-

lated long enough to evolve its respective cohort of autapomorphies.

The sister group relationship between *Urceolina* and *Caliphruria* also seems to be a robust cladistic hypothesis, with *E. oxyandra* potentially ancestral to both. *Eucharis oxyandra* is a taxonomically perplexing species in its characters of morphological intermediacy (androecium and pollen morphology) between *Eucharis* and *Urceolina*. It is known only from bulbs found in local, transient cultivation in Peru, near the single recorded point of geographic sympatry between *Eucharis* (*E. amazonica*) and *Urceolina* (*U. microcrater*). The absence of much character state data, but particularly those on fruit and seed morphology, further occludes resolution of its phylogeny, and any of several hypotheses concerning its origins are possible (see Taxonomic Treatment). *Eucharis lehmannii*, which usually resolves within a cladistic "no man's land" between paraphyletic subg. *Heterocharis* and all other clades, presents a similar problem, though Regel's (1889) figure strongly suggests affinity to subg. *Eucharis*. In the initial analyses, in which all multistate characters were treated as unordered, this poorly known species resolved as sister group to *E. bouchei*. I believe that *E. lehmannii* is a sister species to *E. caucana*, to which it bears much phenetic resemblance, and that its unusual resolution in the cladogram is a result of the great deal of missing character state data. Fruit and seed morphology clearly place *E. caucana* in subg. *Eucharis*, even though it shows as much novelty as *E. oxyandra* or *E. lehmannii* in other characters.

Excluding *E. lehmannii* and *E. oxyandra*, *Eucharis* subg. *Eucharis* forms another clearly monophyletic group. Species with five flowers and two ovules per locule (*E. astrophiala*, *E. cyaneosperma*, *E. ulei*, along with the tetraploids, *E. bonplandii* and *E. bouchei*) form a very natural group with karyotypic similarity as well (Meerow, 1987b). The sister species relationship of *Eucharis caucana* to *E. astrophiala* within this group may be as equivocal as the basal resolution of *E. lehmannii*, since it is based on two apomorphies (pollen size and lack of staminal dentation), the latter of which is highly homoplasious. I believe the reversal in ovule number necessary for *E. caucana* to share common ancestry with *E. astrophiala* is very unlikely.

Eucharis candida and *E. formosa*, two often sympatric (and possibly sibling) species, are cladistically close and basal to the five-flowered clade. The small-flowered species (*E. castelnaeana*, *E. corynandra*, and *E. plicata*) form another very

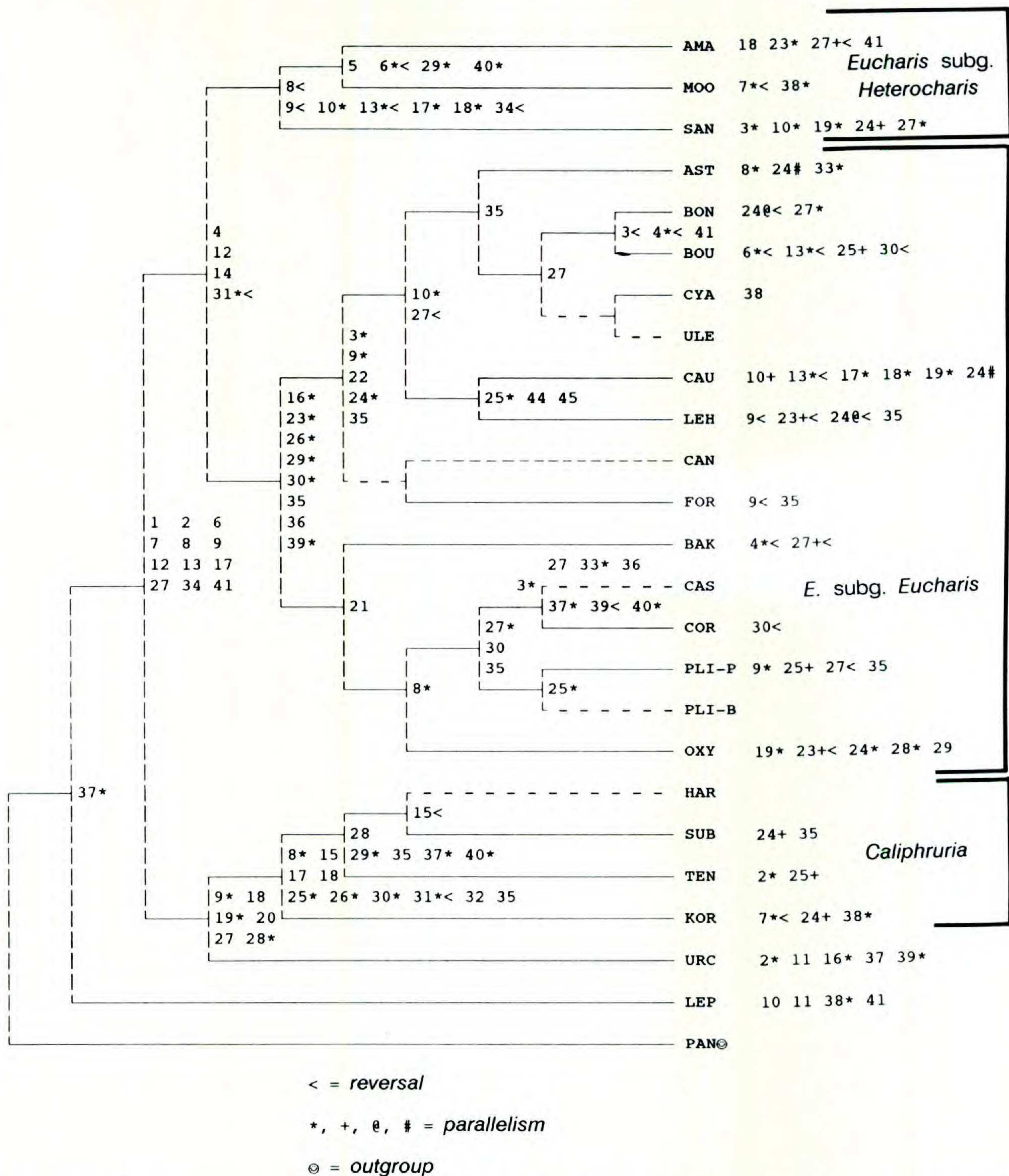


FIGURE 66. User-generated cladogram of *Eucharis* and *Caliphruria*. Broken horizontal line indicates zero-length branch. Numbers inside refer to apomorphies of adjacent EU or internal node. Refer to Table 1 for EU designations.

natural group. The position of *E. bakeriana* as basal to this clade, largely on the basis of a plicate staminal cup, may be equivocal. Karyotype analysis (Meerow, 1987b) suggests putative relationship of *E. bakeriana* to *E. formosa*.

An alternative hypothesis of phylogenetic relationship is presented in Figure 66. The cladogram is a user-generated tree in which *Caliphruria* and *Urceolina* are placed as sister groups to a monophyletic *Eucharis*. The topology of subg. *Eucharis* in this cladogram represents my concepts of their evolutionary relationships based on phenetic resemblance, phytogeography, and chromosome data.

The major differences from the cladogram in Figure 65 are the sister species relationship of *E. caucana* and *E. lehmannii*, the ancestral node of which forms a monophyletic group with the five-flowered, two-ovuled species complex; and the positioning of *E. oxyandra* as part of the small-flowered species group of subg. *Eucharis*. This user-generated cladogram had a length of 100.6 steps, with a CI of 0.443. There are 82 parallelisms represented among the character state changes, and 29 reversals. The user-generated tree (Fig. 66) is thus somewhat less parsimonious than the cladogram in Figure 65. Of particular interest in the user-gen-

erated cladogram is the resolution of the larger monophyletic groups constituting genera or subgenera, and the accompanying character state changes within these clades.

In Figure 66, a monophyletic subg. *Heterocharis* is supported by seven apomorphies, four of which are reversals (unordered characters not counted). Some of these reversals are very unlikely (e.g., reversal to larger, heavily fragrant flowers; see previous discussion of ordered characters) and would thus represent retention of ancestral states.

In the user-generated tree, a monophyletic subg. *Eucharis* is supported by a greater number of apomorphies (eight in Fig. 66) than in the parsimony cladogram (three). *Caliphruria* as a monophyletic group is best supported by Figure 66 (ten apomorphies) versus eight in Figure 65.

The results of these various cladistic treatments illuminate the problems inherent in phylogenetic reconstruction of large, "messy" character state data sets, and particularly with taxa whose evolution has involved large-scale homoplasy. The user-generated cladogram in Figure 66 represents my preferred hypothesis of phylogeny within the *Eucharideae*; nonetheless I cannot deny the compelling evidence that *Eucharis*, by the inclusion of subg. *Heterocharis*, may be paraphyletic.

From an orthodox cladistic perspective (Wiley, 1981), Traub's (1971) concept of a single polymorphic genus, *Urceolina*, is supported by the criterion of parsimony. From a phenetic (and pragmatic) standpoint, I find this unsatisfactory due to the close phenetic relationship between subg. *Heterocharis* and *Eucharis*. This relationship is most conspicuous if one compares *Eucharis bakeriana* and *E. formosa* (the most basal species of subg. *Eucharis*) with *E. amazonica* and *E. moorei* (subg. *Heterocharis*). I prefer to recognize *Urceolina* and *Caliphruria* as distinct genera, despite the attendant risk of a paraphyletic *Eucharis*. I do not believe that *Urceolina* and *Caliphruria* necessarily share an immediate common ancestor—the three apomorphies that define their sister group relationship in Figure 65 (reversal to straight tubes, flower habit, and smaller pollen grains) are homoplasious within the *Eucharideae* as well as in other tribes of the Pancratioidinae (Meerow, 1987c; Meerow & Dehgan, 1985). Until further data allow a more accurate understanding of their relationships, I also prefer to maintain *E. lehmannii* and *E. oxyandra* as species of *Eucharis* subg. *Eucharis*, allied with the small-flowered species with numerous ovules per locule. Without study of living material, and particularly knowledge of fruit char-

acters, I am unwilling to declare *E. oxyandra* a sister taxon to *Urceolina* and *Caliphruria*.

Ashlock (1971, 1972, 1979, 1984) has repeatedly argued for the acceptance of paraphyletic groups in evolutionary systematic classifications. He defined two subclasses of monophyletic groups: holophyletic, which contain all descendants of the stem ancestor, and paraphyletic, those which do not. Ashlock (1979: 449) rejected "the automatic conversion of the cladogram into a classification." Meacham & Duncan (1987) have elaborated on the term "convexity," first proposed by Estabrook (1978), which attempts to resolve the concepts of monophyly, holophyly, and paraphyly. Meacham & Duncan concluded that Ashlock's (1979) advocacy of overall evolutionary similarity as a component of classification schemes, rather than strict cladistic topology alone, is sound, and they discussed the mitigating factors surrounding cladistic methodology (e.g., uncertainty of character state polarities, the speculative nature of phylogenetic reconstructions, among others) which compromise a direct translation of cladogram into classification. A similar argument was recently articulated by Cronquist (1987). Donoghue & Cantino (1988) and Humphries & Chappill (1988) have responded vociferously to Cronquist's (1987) critique. Donoghue & Cantino (1988: 108) assail paraphyletic higher taxa as "artificial classes created by taxonomists who wish to emphasize phenetic 'gaps', and that formal recognition of such taxa conveys a misleading picture of common ancestry and character evolution."

The enormous amount of homoplasy evident within the highly canalized Amaryllidaceae creates great difficulty in phylogenetic reconstruction (Meerow, 1985, 1987c). In the analyses of *Eucharis* and related genera, missing character state data further weaken the argument for adopting ad hoc the most parsimonious phylogeny as the basis for classification. At present, I prefer to accept a less parsimonious phylogeny as represented by the user-generated topology in Figure 66 until such time as cladograms can be generated with consistency indices greater than 0.5. Towards this end, work is continuing with careful application of selected character weighting (Neff, 1986; Wheeler, 1986).

In three neotropical lineages of the Pancratioidinae, parallel trends in the evolution of floral morphology have occurred (Meerow, 1985, 1987c). In each case, taxa with smaller, tubular or ventricose, brightly colored flowers with reduced staminal connation, and without noticeable fragrance

have apparently diverged from taxa possessing a large, white, fragrant, crateriform flower with a staminal cup (Meerow, 1985, 1987c). Each lineage appears to be a monophyletic group on the basis of vegetative and ovarian morphology, as well as chromosome number (Meerow, 1985, 1987c; Traub, 1963). A similar pattern occurs in all three lineages: 1) floral morphology of "derived" taxa suggests an ornithophilous pollination syndrome, and 2) "derived" taxa are found, entirely or in part, at higher elevations than apparent ancestral taxa. *Eucharis* and *Urceolina*, as documented in this paper, present one such case. *Pseudostenomesson* Velarde, submerged by Traub (1980) into *Hymenocallis* as section *Artema*, presents a parallel situation within the *Hymenocallis* lineage (Meerow, 1985; Meerow & Dehgan, 1985). Tribe *Stenomessae* contains two small genera, *Pamianthe* and *Paramongaia*, with ancestral floral morphology and contains a large genus, *Stenomesson*, with derived morphology (Meerow, 1987c). In the *Hymenocallis* and *Eucharis* lineages, the pancratioid floral morphology has radiated to a far greater extent than the putatively ornithophilous divergence (*Pseudostenomesson* and *Urceolina*, respectively). In the *Pamianthe-Paramongaia/Stenomesson* lineage, the derived genus, *Stenomesson* (35–40 species), has speciated to a greater degree than taxa with the ancestral pancratioid flower (*Pamianthe*: 2 species, *Paramongaia*: monotypic).

The high level of divergence in neotropical pancratioid tribes may be primarily a factor of two causes, 1) the uplift of the Andes in the Pliocene (van der Hammen, 1974, 1979), creating much opportunity for geographic isolation, and 2) greater genetic adaptability via tetraploidy to new ecological zones. The occurrence of rare hybridization in nature between the relict complex represented by *Eucharis* subg. *Heterocharis* and both *Caliphruria* (\times *Calicharis butcheri*) and *Urceolina* (\times *Urceocharis edentata*) may be further indication that the evolution of these genera was geologically recent.

TAXONOMIC TREATMENT

SUBSPECIFIC TAXA

The rank of subspecies is used once in this treatment (*E. plicata*) to designate strong morphological divergence coupled with geographical isolation that I accept within specific limits. The rank of variety is used in a case (*E. bouchei*) where both the morphological and geographic components

of divergence are weaker but appear to represent the first stages of speciation within a tetraploid semispecies complex (Meerow, 1987d).

CRITICAL MEASUREMENTS

Measurements of vegetative and floral parts in the following species descriptions are derived from examination of dried material (floral parts after rehydration in 3% solution of Aerosol OT brought to boil) supplemented with examination of fresh or FAA-preserved material when available. I found less than 5% difference between measurements of dried and fresh or spirit-preserved material of the same collection when available.

A NOTE ON THE KEYS

Species of *Caliphruria* and *Eucharis* subg. *Heterocharis* are separable by discrete characters very amenable to key construction. Using the keys to these two groups, any worker should be able to identify material referable to described taxa whether in the field or the herbarium. The enormous degree of variation exhibited by species of subg. *Eucharis*, however, made key construction difficult. A number of the species overlap to at least some degree with one or more other species in virtually all quantitative morphological characters. As a consequence, sometimes I have had to rely on characters observable only with living material. With perseverance, it should be possible to key out all but the most depauperate herbarium specimens of subg. *Eucharis*. Collectors should note such characters as leaf plication and undulation, floral fragrance, tepal habit, and pigmentation and plication of the staminal cup in their notes when preparing specimens of *Eucharis*.

KEY TO EUCHARIS AND CALIPHRURIA

- 1a. Leaf margins usually undulate; flowers declinate to pendulous via the curving of the tube; perianth funnelform-campanulate or crateriform; tube cylindrical, at least below middle, abruptly dilating at or above the midpoint of its length, curved, 25–50 mm long; staminal cup conspicuous, basally pigmented green or yellow, exerted from the throat of the perianth or adnate to the dilated portion of the tube; stigmatic papillae unicellular *Eucharis*
- 1b. Leaf margins nonundulate; flowers declinate to subpendulous via the curving of the pedicel; perianth funnelform; tube funnelform, dilating gradually from base (rarely subcylindrical), straight or only slightly cernuous, 25 mm or less long; staminal cup inconspicuous and unpigmented, reduced to a membranous, basal

connation of the filaments; stigmatic papillae multicellular *Caliphuria*

Eucharis Planchon et Linden, Linden's Ann. Cat. Hort. 8: 3. 1852; Fl. des Serres Jard. Eur. Ser. 1, 8: 107. 1853. TYPE: *Eucharis candida* Planchon et Linden. *Urceolina* subg. *Eucharis* (Planchon & Linden) Traub, Pl. Life 27: 57-59. 1971.

Evergreen, bulbous geophytes of rain forest understory. Bulb tunicate, usually offsetting vigorously. Leaves petiolate, persistent, glabrous; petiole subterete, somewhat concave adaxially proximal to the sinus, convex abaxially, light green, winged distally by attenuation of the lamina; lamina ovate, elliptic, ovate- or elliptic-lanceolate, usually thin, predominantly hypostomatic, usually lustrous, dark green adaxially, light or silvery green abaxially, smooth or plicate between the parallel veins, cuticle of the abaxial epidermis variably striate, margins frequently undulate, apically acute or acuminate, basally attenuate to the petiole, rarely appearing subcordate. Inflorescence scapose, umbellate (composed of 1 to several reduced helicoid cymes); scape solid, terete or slightly compressed, glaucous, terminating in 2 green or greenish white, ovate-lanceolate, valvate-imbricate, marcescent bracts enclosing the flowers and several secondary bracts before anthesis. Flowers 2-10(-12), pedicellate (rarely sessile), each subtended by a lanceolate bracteole, pendent or declinate, sometimes fragrant, white, usually protandrous; perianth crateriform or campanulate; tube cylindrical, dilating abruptly above its midpoint, sometimes stained green proximally; limb of 6 tepals in 2 series spreading widely from the throat or imbricate for half their length, the outer series usually longer, narrower and apiculate; the inner series acute, obtuse, or minutely apiculate. Stamens 6, variously connate below, pigmented yellow or green proximally; free filament linear, subulate, or otherwise petaloid; anthers oblong to linear, sub-basifixed or dorsifixed, eventually becoming versatile, introrse, dehiscing longitudinally; pollen grain boat-shaped elliptic, monosulcate, the exine reticulate. Style filiform, included within, equal to, or exerted from the staminal cup; stigma obtusely 3-lobed, papillose. Ovary inferior, green or white, globose-ellipsoid, oblong, occasionally trigonous, 3-locular; septal nectaries present; ovules 2-20 per locule, placentation axile, globose, anatropous. Fruit a 3-lobed, loculicidal capsule, thin-walled or leathery, green or bright orange; seed globose or ellipsoid, sometimes angled by pressure, turgid, with copious en-

dosperm, few per locule; testa thin, phytomelanous, lustrous (rarely dull) black, dark brown or blue, usually smooth. Chromosome numbers: $2n = 46, 68, 92, 138$.

KEY TO THE SUBGENERA OF *EUCHARIS*

- 1a. Flowers 3-7 cm long, usually pendulous, only rarely and mildly fragrant, crateriform (rarely somewhat campanulate); perianth tube cylindrical below, dilated abruptly just below the throat (rarely in the upper $\frac{1}{4}$), usually strongly curved, white; limb segments usually spreading widely (ca. 90°) at perianth throat; staminal cup inserted at throat of tube, proximally spotted or stained yellow, green, or yellow-orange equally on the exterior and interior of the cup; distal portion of filament usually widely subulate (> 1.5 mm wide) or otherwise petaloid; anthers \pm erect at anthesis; ovules 2-9(-10) per locule; capsule leathery and bright orange (rarely green, in which case tardily dehiscent)
..... *Eucharis* subg. *Eucharis*
- 1b. Flowers 7-8 cm long, declinate or subpendulous, strongly fragrant, funnelform-campanulate to crateriform; perianth tube cylindrical below, dilated abruptly at $\frac{1}{3}$ - $\frac{1}{2}$ its length, green (at least proximally); limb segments usually imbricate for half their length; staminal cup partially adnate to upper portion of tube, sometimes reduced, flushed (yellow-)green, particularly along the filamental traces, with the pigmentation most intense on the interior of the cup; distal portion of the filament usually narrowly subulate (≤ 1 mm wide); anthers versatile at anthesis; ovules (7, 9-)16-20 per locule
..... *Eucharis* subg. *Heterocharis*

Eucharis subg. **Eucharis**

Leaves glabrous, petiolate, persistent; lamina ovate, elliptic, or lanceolate, mostly thin, margins usually undulate, variably plicate between the parallel veins, apically acute or acuminate, basally attenuate to the petiole or rarely subcordate, mostly dark green and lustrous adaxially, light or silvery green abaxially, the abaxial epidermis variously striate; petiole subterete, somewhat channeled adaxially proximal to the sinus. Inflorescence scapose, umbellate, terminating in 2 greenish white marcescent bracts. Flowers pedicellate, (3-)5-10, only rarely with noticeable fragrance, mostly pendulous, 3-7 cm long, crateriform (rarely slightly campanulate); perianth tube usually strongly curved, cylindrical below, dilated just below the throat or rarely at $\frac{1}{3}$ length, white; limb of 6 white, ovate to ovate-lanceolate tepals usually spreading widely from the throat, often recurved above the middle, the outer 3 usually longer, narrower, and apically apiculate, the midvein often faintly yellow in strong light. Stamens connate into a conspicuous

or rarely reduced staminal cup, usually exerted from the rim of the throat; staminal cup apically white, marked green or yellow (rarely yellow-orange) basally, variously toothed, lobed or entire; distal portion of the filaments petaloid and variously shaped; anthers oblong or linear, subdorsifixed or sub-basifixed, \pm erect at anthesis, finally becoming versatile; pollen grain 45–60 μ m (polar axis), 55–86 μ m (longest equatorial axis), the exine coarsely reticulate. Style filiform, white; stigma obtusely trilobed, glandular pubescent. Ovary globose, elliptic or trigonous, green or white; ovules globose to

ellipsoid, axile, superposed, 1–12 per locule, most often 2–4. Fruit a loculicidal capsule, orange and leathery when ripe (rarely remaining green); seeds 1–3(–4) per locule, ca. 1 cm long, turgid, ellipsoid (rarely somewhat compressed), with a lustrous black or blue testa.

Distribution. Fourteen species, (Guatemala) Costa Rica to Bolivia, concentrated on the lower slopes of the northeastern Andes and western Amazonas, usually below 1,000 m.

KEY TO THE SPECIES OF *EUCHARIS* SUBG. *EUCHARIS*

- 1a. Perianth tube 25 mm or more long.
 - 2a. Flowers (7–)8–10 (or very rarely 5); ovules 3–9 per locule (or very rarely 2).
 - 3a. Flowers not fragrant; perianth tube (25–)30–35 mm long; outer tepals (20–)25–30(–33) mm long; staminal cup 8–11 mm long to apex of teeth or lobes; ovules (2–)3–5(–7) per locule 1. *E. candida*
 - 3b. Flowers mildly fragrant; perianth tube 35–45(–50) mm long; outer tepals (28–)32–45(–47) mm long; staminal cup 10–16 mm long to apex of teeth or lobes; ovules (2–4)7–9 per locule.
 - 4a. Floral fragrance slightly fetid; flowers pendent; staminal cup less than 15 mm long to apex of teeth or lobes, cleft 3–5 mm between each stamen, nonplicate; staminal teeth (if present) much less than half the length of the subulate portion of the filament; style exerted ca. 1 cm beyond the anthers 2. *E. formosa*
 - 4b. Floral fragrance sweet; flower perpendicular to vertical axis of scape; staminal cup more than 15 mm long to apex of teeth, cleft very shallowly (less than 2 mm) between each stamen, plicate; staminal teeth half the length of the subulate portion of the filament; style exerted less than 0.5 cm beyond the anthers 3. *E. bakeriana*
 - 2b. Flowers 2–5(–7); ovules 2–3(–5) per locule.
 - 5a. Leaves nonplicate, somewhat succulent, margins nonundulate, length-to-width ratio usually less than 3; petiole usually shorter than the lamina; plants of central and western Colombia or Central America.
 - 6a. Leaves slightly glaucous adaxially; abaxial cuticle densely striate; perianth tube 25–33 mm long; staminal cup irregularly toothed, proximally pigmented pale yellow; stamens always constricted distally into a narrow subulate portion; style exerted less than 0.5 cm beyond anthers; ovary not trigonous; plants of Colombia 4. *E. bonplandii*
 - 6b. Leaves not glaucous; abaxial cuticle largely devoid of striations; perianth tube (25–)33–45 mm long; staminal cup most frequently edentate, proximally pigmented green; stamens often dilating gradually from apex to base; style exerted 0.5–1 cm beyond anthers; ovary often trigonous; plants of Central America 5. *E. bouchei*
 - 5b. Leaves plicate, thin, margins undulate, lamina length-to-width ratio usually greater than 3; petiole usually equal to or longer than the lamina; plants of western Ecuador, Colombia, or Amazonas.
 - 7a. Leaves bullate-pustulate in texture, nonlustrous; staminal cup pigmented yellow-orange proximally; stamens deltoid, dilating gradually from apex to base; ovary white; plants of western Ecuador 6. *E. astrophiala*
 - 7b. Leaves not bullate-pustulate in texture, lustrous; staminal cup pigmented yellow or green; stamens not deltoid, constricted distally into a narrow (less than 2 mm wide) subulate portion; ovary green; plants of western Colombia or Amazonas.
 - 8a. Perianth funnelform-campanulate, tube dilated distally at approximately $\frac{1}{3}$ its length; staminal cup inconspicuous; filaments connate proximally for 3 mm or less; plant of western Colombia 7. *E. caucana*
 - 8b. Perianth crateriform, tube dilated abruptly just below the throat; staminal cup conspicuous; filaments connate proximally for 8 mm or more; plants of Amazonas.
 - 9a. Perianth tube curved gradually throughout the proximal half; staminal cup usually bidentate but sometimes obtusely lobed (rarely one to several stamens quadrate); ovary globose-elliptic at anthesis; testa lustrous black 8. *E. ulei*
 - 9b. Perianth tube usually curved abruptly above the ovary, then more or less straight for the rest of its length; staminal cup usually quadrately lobed, but one or several stamens occasionally toothed; ovary deeply trigonous at anthesis; testa lustrous blue 9. *E. cyaneosperma*
 - 1b. Perianth tube equal to or less than 25 (or very rarely to 30) mm long.
 - 10a. Staminal cup usually less than 1 cm long to apex of teeth or lobes, but connate portion of filaments always much shorter than free, subulate portion.

- 11a. Teeth of the staminal cup acutely long-lanceolate, as long as the subulate portion of the filament; ovules 10 per locule, plants of western Colombia 10. *E. lehmannii*
- 11b. Teeth of the staminal cup (when present) obtuse, much shorter than the subulate portion of the filaments; ovules fewer than 10 per locule; plants of the Peruvian east Andes.
- 12a. Staminal cup 3.5 mm long (to apex of teeth), obtusely bidentate between each stamen; free filaments club-shaped (appearing elliptic-lanceolate in dried material), 1.8–2 mm wide, ovules 4–6 per locule 11. *E. corynandra*
- 12b. Staminal cup reduced to a basal connation of the filaments 0.8–1.5 mm long, edentate or obtusely bidentate; free filaments narrowly subulate, ca. 1 mm wide; ovules 6–8 per locule 12. *E. oxyandra*
- 10b. Staminal cup usually greater than 1 cm long to apex of teeth or lobes, but connate portion of filaments always longer than the free, subulate portion.
- 13a. Leaves 7–12(–14) cm wide; staminal cup campanulate, gradually dilating distally, plicate along the filamental traces; ovary green; capsule leathery, bright orange, dehiscent; seeds ellipsoid, with a lustrous, smooth black testa 13. *E. plicata*
- 13b. Leaves 3–6 cm wide; staminal cup funnelform-cylindrical to cylindrical, often abruptly dilated distally at $\frac{1}{2}$ – $\frac{2}{3}$ length, plicate between the filamental traces; ovary whitish; capsule green, thin-walled, often tardily dehiscent; seeds wedge-shaped, with a dull, rugose black testa 14. *E. castelnaeana*

1. *Eucharis candida* Planchon et Linden, Linden's Ann. Cat. Hort. 8: 3. 1852; Fl. des Serres Jard. Eur. Ser. 1, 8: 107. 1853. TYPE: ex hort. Linden, supposedly imported from Colombia, no other data, *Planchon s.n.* (MPU). *Urceolina candida* (Planch. & Lind.) Traub, Pl. Life 27: 57–59. 1971. Figures 67–69, 70A.

Bulb subglobose, 3–5(–6) cm long, 3–4(–5) cm diam., neck 1–2.5(–4) cm long, 1–2.5 cm wide; tunics brown. Leaves 1–2, petiole (15–)18–30(–35) cm long, ca. 7 mm thick proximally, ca. 3–4 mm thick distally; lamina elliptic, (18–)30–35 cm long, (7–)8.5–11.5(–12) cm wide; acuminate, deeply plicate, dark green but only slightly lustrous adaxially, light green abaxially, abaxial cuticle striate, the margins coarsely undulate. Scape (4–)5–6 dm tall, 8–10 mm diam. proximally, 4–5 mm diam. distally; bracts 25–45(–50) mm long, ca. 5–6 mm wide, ovate-lanceolate. Flowers (7–)8–10, rarely as few as 5, without noticeable fragrance; pedicels (9–)15–20(–35) mm long; tube (25–)30–35 mm long, ca. 2 mm diam. for most of its length, abruptly dilated to (7–)10(–11.5) mm at the throat; limb spreading to 4.5–6 cm wide; tepals sometimes recurved distally, outer tepals (20–)25–30(–33) mm long, (9–)10.5–14(–15) mm wide, ovate-lanceolate, apiculate, the apiculum only slightly or obscurely tufted adaxially; inner series (20–)22–28(–32) mm long, (10–)12–15(–20) mm wide, ovate, acute to minutely apiculate. Staminal cup funnelform-cylindrical to slightly campanulate, rarely widely ampliate distally, (7–)8–11 mm long (to apex of teeth or lobes), (10–)13–16(–18) mm wide, most frequently edentate and lobed between each stamen, at times bidentate or irregularly toothed, widely spotted green to greenish yellow

below each stamen; teeth, when present, 1–2 mm long, < 1 mm wide, acute or obtuse; cup cleft for (2.5–)3–5(–6) mm between each stamen; stamens (3.5–)4.5–5.5(–6) mm wide proximally; distal subulate portion (3.5–)4.5–6(–6.5) mm long, 1.5–2 mm wide at the base; anthers (3.5–)4–5(–6) mm long, oblong; pollen grain 46.8–50 μ m polar diam., 68.7–73 μ m longest equatorial diam. Style (38–)45–55 mm long, exerted 0.5–1 cm beyond the anthers; stigma 2–d3 mm wide. Ovary globose-ellipsoid, green, 5–7(–8) mm long, 4–6(–7) mm diam.; ovules (2–)3–5(–7) per locule. Capsule (1.5–)1.8–2.4 cm long, (2–)2.5–2.9 cm wide, bright orange, leathery; pedicel 2–4 cm long; seeds 1–2(–3) per locule, ellipsoid, ca. 1 cm long, ca. 0.5 cm diam., with a lustrous, smooth black testa. Chromosome number: $2n = 46$.

Distribution. Understory of primary rain forest chiefly in the Oriente of Ecuador, particularly the Río Napo valley, occasional in north Peru and southeast Colombia (Figs. 71, 72) at (100–180)240–550(1,000–1,600) m. Flowering at any time of the year, most frequently in February, March, and August.

Vernacular name. Cebolleta.

Additional specimens examined. COLOMBIA. AMAZONAS: Puerto Nariño, 24 Jul 1965, *Lozano et al.* 594 (COL); Trapecio amazonica, Loretoyacu River, ca. 100 m, Oct. 1946, *Schultes & Black* 8478 (US). META: sabanas de San Juan de Arama, margen izquierda del Río Güejar, alrededores del aterrizaje "Los Micos," 500 m, 22 Jan. 1951, *Idrobo & Schultes* 1208 (COL, GH, NY, US). PUTUMAYO: vicinity Mocoa, Río Rumiaco, 1,100 m, 8 Oct. 1959, *Barclay & Juajibioy* 9461 (MO). ECUADOR. NAPO: Tena, wet forest, 27 Sep. 1939, *Asplund* 8853 (S); El Napo, 1931, *Benoist* 4717 (P); Río Yasuni, 12 km from mouth at Río Napo, 0°57'S, 75°25'W, 200 m, 25–26 Aug. 1982, *Balslev & Alarcon* 2966 (QCA);

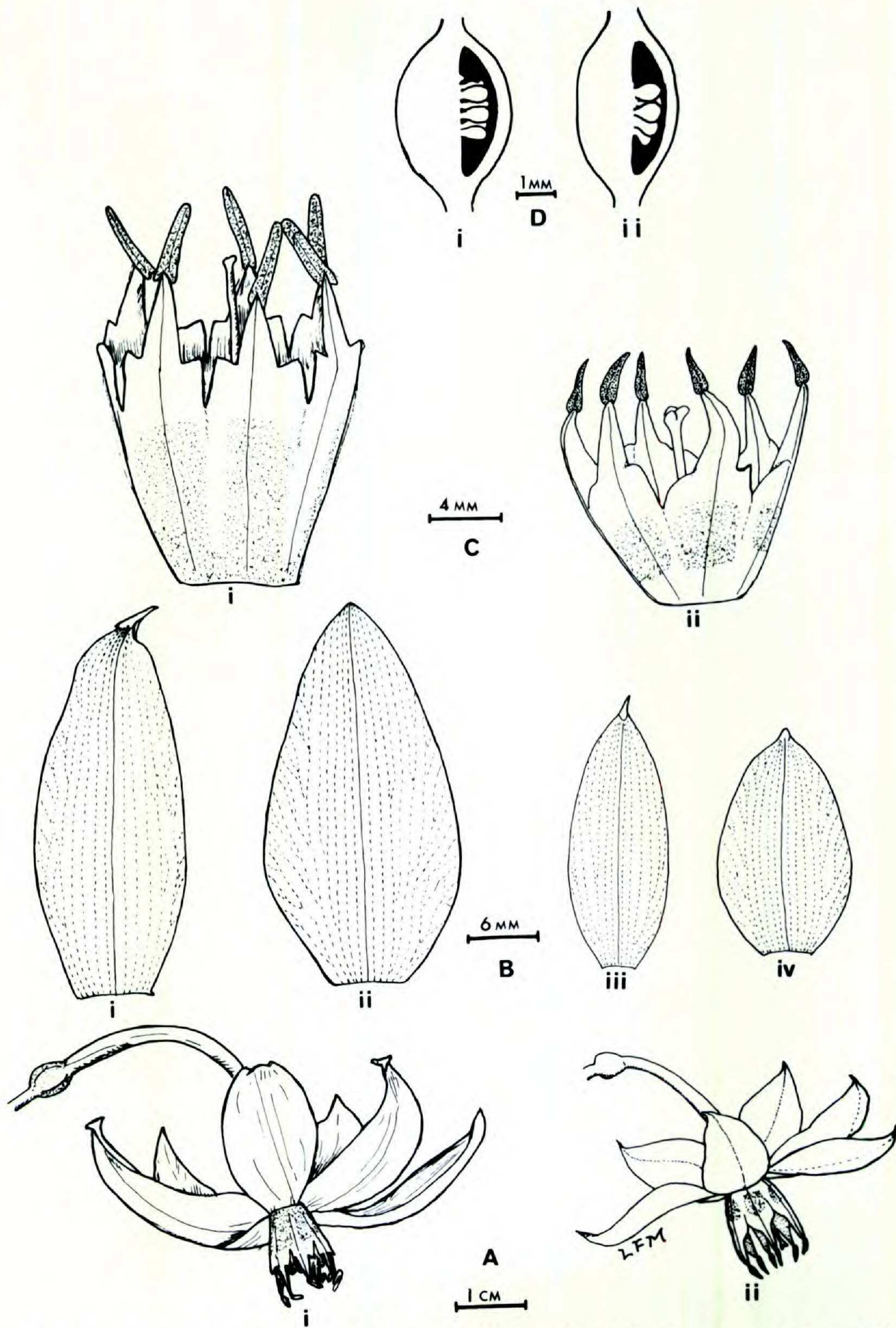
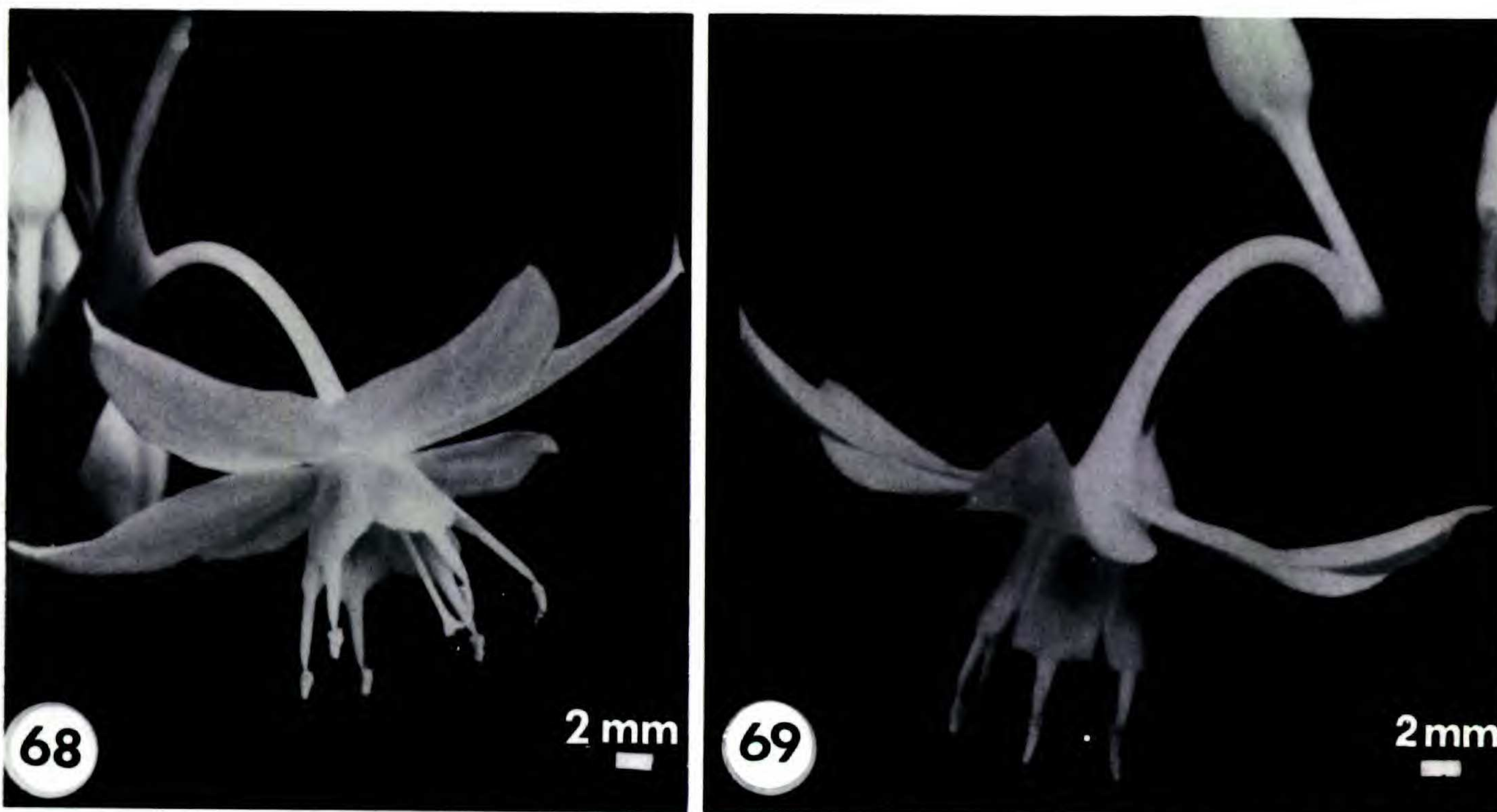


FIGURE 67. *Eucharis formosa* (Meerow 1103, FLAS) and *E. candida* (Dodson et al. 14095, SEL).—A. Flowers. i, *E. formosa*; ii, *E. candida*.—B. Tepals. i, ii, *E. formosa*. i, outer tepal; ii, inner tepal. iii, iv, *E. candida*. iii, outer tepal; iv, inner tepal.—C. Staminal cups. i, *E. formosa*; ii, *E. candida*.—D. Ovaries, longitudinal section. i, *E. formosa*; ii, *E. candida*.

70 km downstream from Coca at Anangu, 260 m, 8–11 Aug. 1982, Besse et al. 1598 (SEL); Tena-Puyo road, 550 m, Aug. 1982, Besse et al. 1643 (SEL); Coca-Lago Agrio road, 45 km north of Coca, Río Palanda Yacu, 7 June 1983, Bohlin & Bohlin 319 (GB); Isla Pompeya, 19 Apr. 1983, Dinua 42 (QCA); km 5, Cotunda-Coca, 1,130 m, 19 June 1963, Dodson et al. 14095 (SEL); orilla izquierda del Río San Miguel, Puerto Nuevo, 26 Mar. 1953, Gutierrez V. 2687 (COL); Santa Rosa at Río Napo, ca. 400 m, 29 Feb. 1972, Harling 11090 (GB); Hacienda Cotapino (Concepción), 550 m, 19–20 Feb. 1968, Harling et al. 7121 (FLAS, GB); lower Río Aguari-

co (above Puesto militar Puerto Loja, 7 Mar. 1968, Harling et al. 7400 (GB); Coca, potreros and rastrojos near the village along road to Lago Agrio, ca. 250 m, 2 Feb. 1974, Harling & Andersson 11682 (GB); Cañon de los Monos, ca. 12 km north of Coca, 250 m, 4 Feb. 1974, Harling & Andersson 11719, FLAS specimen (FLAS); Misahualli at Río Napo, 28 Mar. 1969, Holguer 925 (FLAS, GB); environs of Limoncocha, 240 m, June 1978, Madison et al. 5326 (F, SEL); between Río Napo and Río San Miguel, 0°30'S, 76–77°W, 300 m, Aug.–Sep. 1978, Navarrete 78. PASTAZA: Mera, forest on shore of Río Pastaza, ca. 1,000 m, 30 Jan. 1956, Asplund



FIGURES 68, 69. Variation in a single Peruvian population of *Eucharis candida* (Schunke 14155-B, FLAS).—68. Flower with wide-spreading staminal cup.—69. Flower with cylindrical staminal cup.

19120 (S); Puyo–Arajuno Road, 1–5 km SW Diez ed Agosto, ca. 900 m, 4 Feb. 1980, *Harling & Andersson 16862* (GB); 68 km north of Puyo on road to Tena, along creek, ca. 500 m, 26 July 1982, flowered in cultivation, 15 Jan. 1985, *Meerow 1144* (FLAS). MORONA-SANTIAGO: Huamboya, 1,500–1,600 m, 15 Feb. 1944, *Acosta-Solis 7469* (F). PERU. AMAZONAS: 400 m atras de La Poza, Río Santiago, 180 m, 23 Aug. 1979, *Huashikat 164* (MO). LORETO: Maynas, Río Ampiyacu, Pebas and vicinity, approx. 3°10'N, 71°49'W, behind Pebas on trail north of town, 10 Apr. 1977, *Plowman et al. 6724* (F); Maynas, Santa María de Nanay, Colonia San Fransisco de Indies Yaguas, 1.5 km del Fundo Balcon, Río Momen, 106–110 m, 15 Nov. 1984, *Schunke 14155-B* (F, FLAS).

Putative hybrids with E. formosa: ECUADOR. NAPO: km 23 Lago Agrio–Baeza road, 350 m, July 1982, *Besse et al. 1558* (SEL); 35 km south of Río Aguatico, Lago Agrio–Coca road, July 1982, *Besse et al. 1563* (SEL); Río Coca, 10 km upstream from ferry crossing, 250 m, 28 Nov. 1983, *Besse et al. 1949* (SEL).

Eucharis candida was originally described from cultivated material supposedly originating from Colombia, a country in which it has been encountered only rarely. The species previously has been delimited by the absence of staminal dentation; however, this character varies considerably throughout the range of *E. candida* (Fig. 70A), as in the related species *E. formosa* and *E. ulei*. Peruvian populations of *E. candida* are variable in the shape of the staminal cup (Figs. 68, 69), even among flowers of the same inflorescence.

Eucharis candida is most common throughout the upper Napo Valley in eastern Ecuador and is very often sympatric with the larger-flowered and

more widely distributed *E. formosa* (Figs. 71, 72). In one instance, two specimens (*Harling & Andersson 11719*), one each of the two species, were collected under the same number. To date, no species of *Eucharis* other than these two have been collected north of the Pastaza valley in eastern Ecuador. On the basis of herbarium study alone, Ecuadorean populations of these two taxa form a mosaic that seemed taxonomically insoluble until living material of both species from several populations was collected and flowered. Phenetic and karyotype analyses (Meerow, in press) support their recognition as distinct species and suggest that *E. candida* and *E. formosa* have hybridized in at least one area of sympatry.

Eucharis candida may be separated from *E. formosa* by its smaller leaves and flowers, complete absence of fragrance (*E. formosa* produces a mild, “sour” odor), and generally fewer ovules per locule (though both species are variable in ovule number). On the basis of known collections, *Eucharis formosa* is slightly better represented in the Pastaza valley than *E. candida*.

2. ***Eucharis formosa*** Meerow, *Sida* 21: 29–49. 1987. TYPE: Ecuador. Morona-Santiago: Road Limón–Macas, ca. km 20 from Limón, primary rain forest and rastrojos, 700–900 m, 26 Mar. 1974, *Harling & Andersson 12915* (holotype, GB; isotype, FLAS). Figures 67, 70B, 73–78.

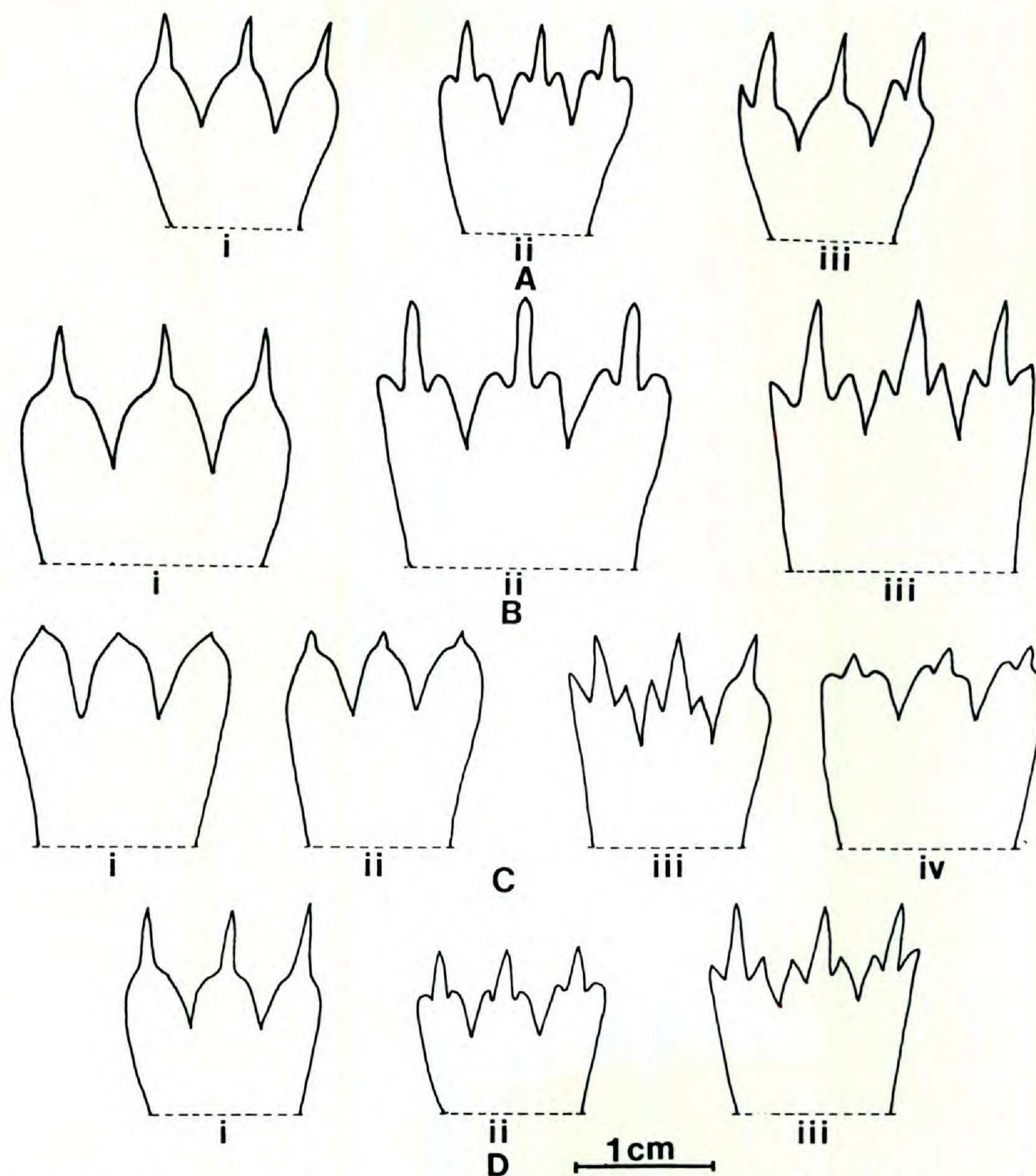


FIGURE 70. Staminal cup variation in four species of *Eucharis*.—A. *E. candida*. i, Besse et al. 1598 (SEL); ii, Harling et al. 7400 (GB); iii, Schultes & Black 8476 (US).—B. *E. formosa*. i, Penland 142 (US); ii, Holguer 2655 (GB); iii, Harling et al. 7201 (GB).—C. *E. bouchei*. i, ii. Variety *bouchei*. i, Lewis et al. 2617 (MO); ii, Allen 120 (US). iii. Variety *dressleri* (Meerow 1107, FLAS). iv. Variety *darienensis* (Gentry & Mori 13945, MO).—D. *E. ulei*. i, Plowman & Kennedy 5811 (GH); ii, holotype, Ule 5737A (B); iii, Schunke 1887 (F).

Bulb subglobose, 4–7 cm long, 3–5 cm diam., neck 2–5 cm long, ca. 1 cm thick, tunics brown. Leaves 1–2(–3); petiole 25–38(–42) cm long, 8.5–1 mm thick proximally, 5–6 mm thick distally; lamina elliptic, (21–)30–45(–52) cm long, (8–)11–15(–16) cm wide, usually conspicuously plicate, dark green and only slightly lustrous adaxially, light green abaxially, abaxial cuticle striate, margins coarsely undulate. Scape (5–)6–7(–8) dm tall, ca. 1 cm diam. proximally, 5–6 mm diam. distally; bracts ovate-lanceolate, (36–)43–60(–85) mm long, 10–15 cm wide at the base. Flowers 8–10, very rarely fewer, pendent, emitting a mild “sour” odor; pedicels (8–)12–18(–30) mm long; tube 35–45(–50) mm long, ca. 2–2.5 mm wide for most of its length, abruptly dilated to (9–)10–13(–14) mm at the throat; limb spreading to (55–)60–70(–80) cm; tepals sometimes recurved distally; outer tepals

narrowly ovate, (30–)35–45(–47) mm long, (10–)15–18(–20) mm wide, apiculate, apiculum conspicuously horned adaxially (Ecuadorian populations); inner tepals ovate, (28–)31–40(–45) mm long, (15–)18–22(–25) mm wide, acute to minutely apiculate. Staminal cup funnellform-cylindrical, 10–13(–15) mm long (to apex of teeth or lobes), (15–)17–20(–22) mm wide; flushed greenish yellow proximally, with the greatest concentration of pigment below each free filament, rarely only widely punctate; bidentate, irregularly toothed, lobed or quadrate between the distal portion of the filament; cup cleft between each stamen for 3–5 mm; teeth when present acute or obtuse, ≤ 2 mm long; each stamen (5–)6–7(–7.5) mm wide tooth to tooth or lobe to lobe; distal portion of filament subulate, (4.5–)5–6.6(–7) mm long, (1.8–)2–2.5(–3) mm wide at point of dilation; anthers oblong,

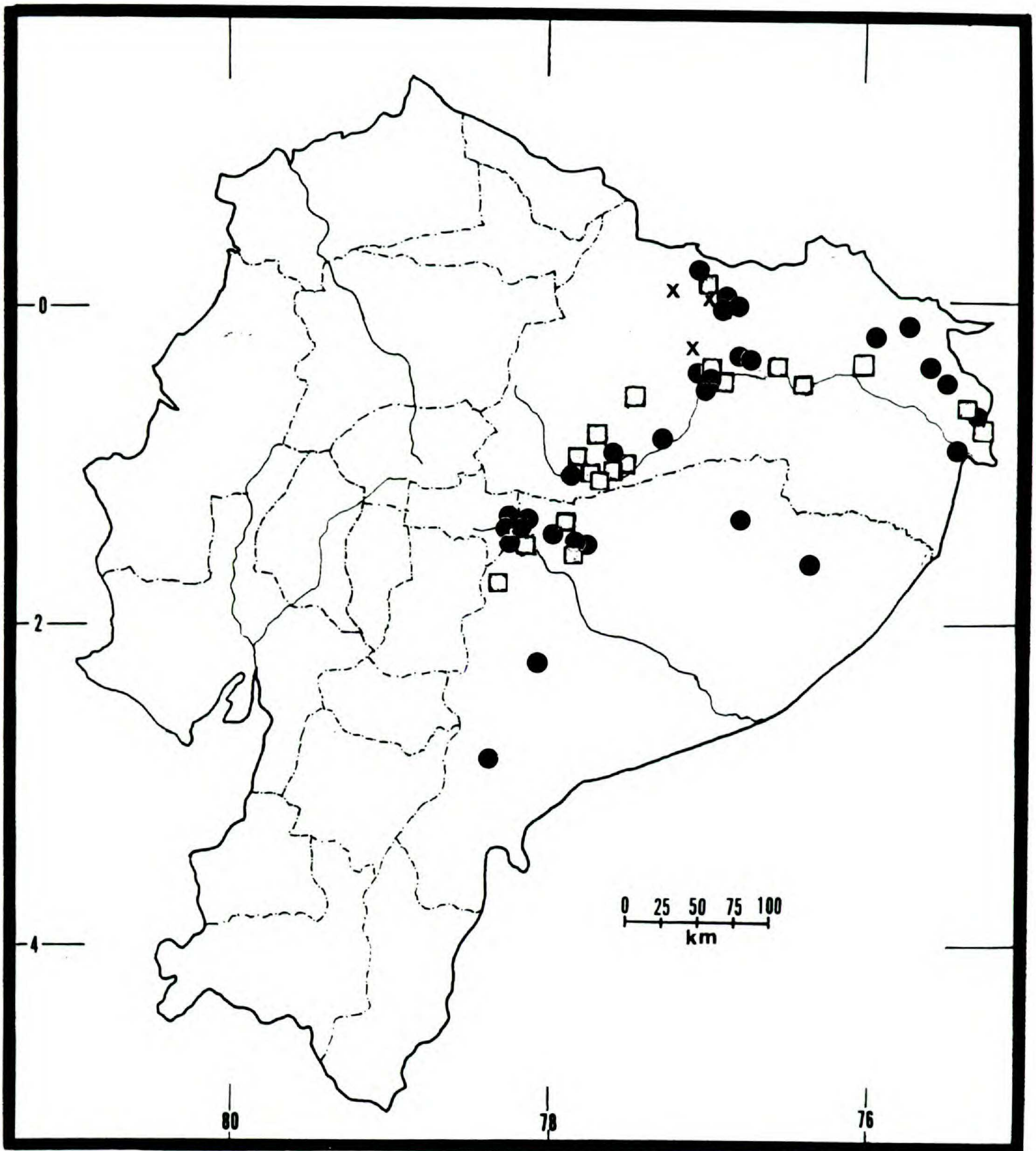


FIGURE 71. Distributions of *Eucharis candida* (squares) and *E. formosa* (circles) in Ecuador. X = *E. candida* × *E. formosa*.

4.5–5.5(–6) mm long, gray-brown; pollen grain 47.7–53.4 μm polar diam., 65.5–73.8 μm longest equatorial diam. Style 5.5–6(–6.5) cm long, exerted ca. 1 cm beyond the anthers; stigma ca. 2–3 mm wide. Ovary globose-ellipsoid, 6–8.5(–10) mm long, (4.5–)5.5–7(–7.5) mm diam., green; ovules (2–)5–7(–8). Capsule 1.5–2 cm long, 2–3 cm wide, bright orange, leathery; pedicels 3–4 cm long; seeds (1–)2–4 per locule, ellipsoid, 8–10 mm long, 5–6 mm diam., with a lustrous, smooth black testa. Chromosome number: $2n = 46$.

Distribution. Rich, moist soil in the understory of premontane and lower montane rain forest, chiefly in the Napo and Pastaza drainage of Ecuador (Fig. 71); less frequent in Amazonian Peru and Colombia, the lower “ceja de la selva” of north-central Peru, and upper Huallaga valley of Peru (Fig. 72); rare in central Colombia (a single, poorly documented, and very disjunct collection (*Killip s.n.*, COL) from near Popayan may be of cultivated origin), 100–1,800 m. Flowering most commonly January–March.

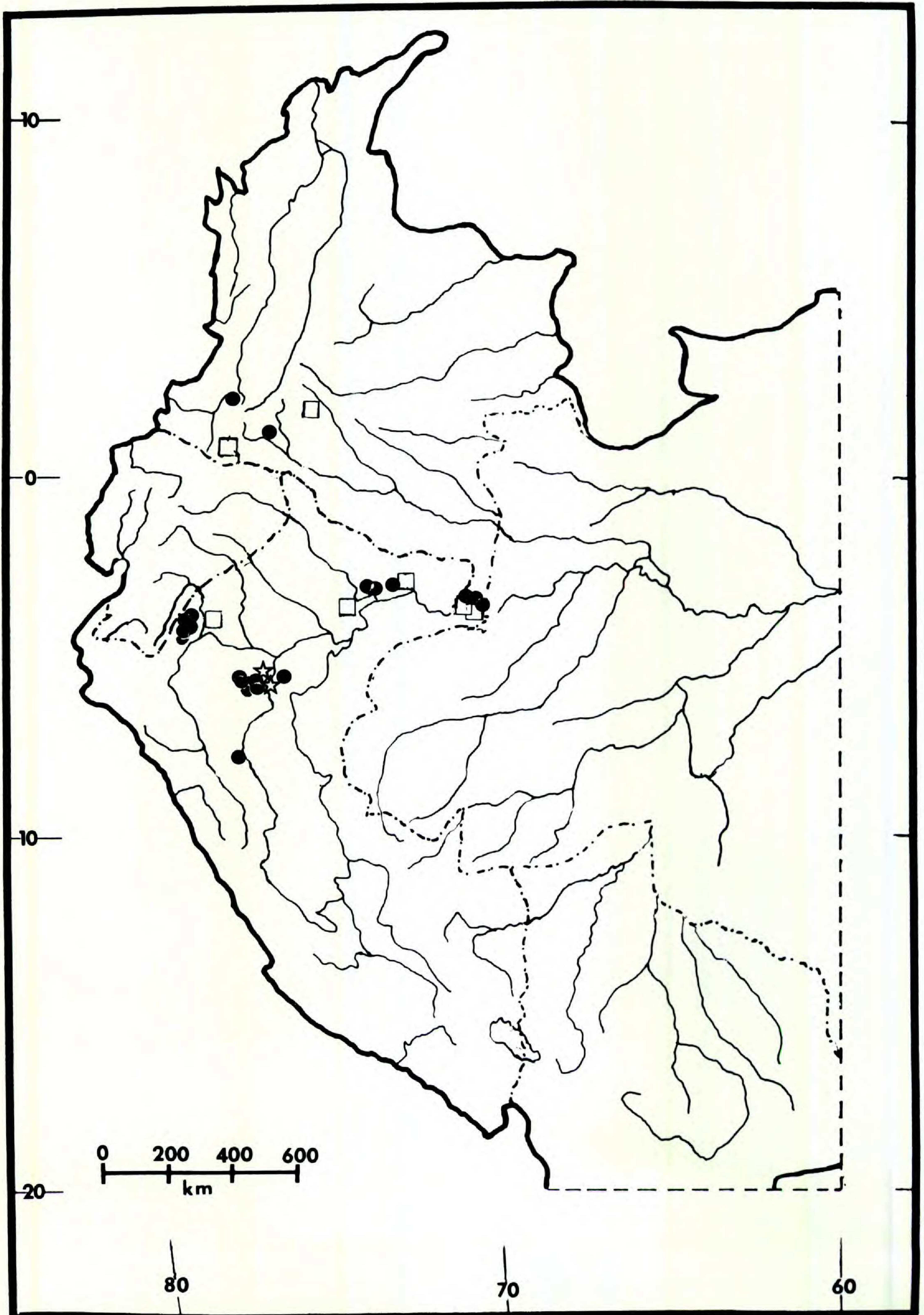
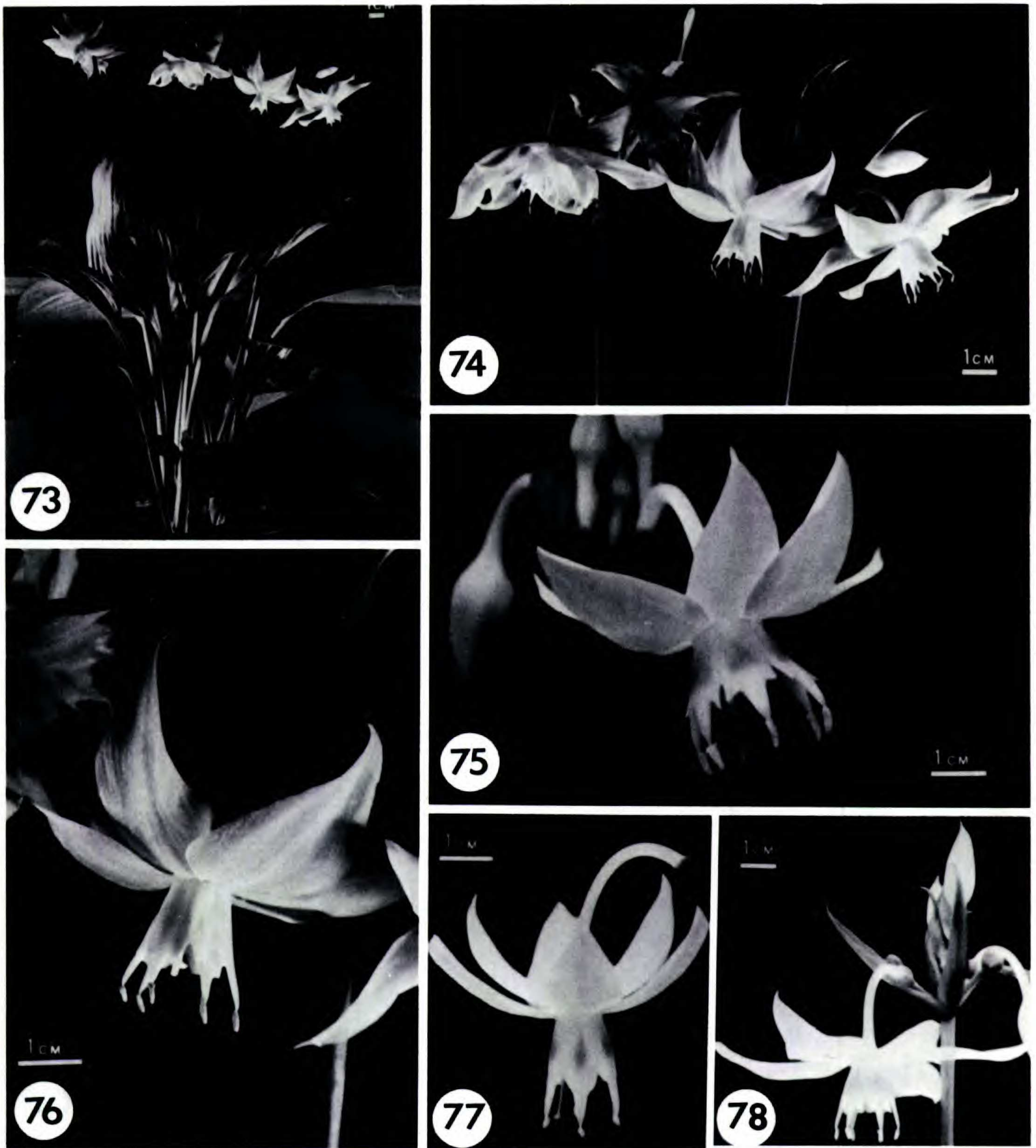


FIGURE 72. Distributions of *Eucharis bakeriana* (stars), *E. candida* (squares), and *E. formosa* (circles) in northwestern-central South America exclusive of Ecuador.



FIGURES 73–78. Variation in *Eucharis formosa*. — 73, 74, 76. Meerow 1103 (FLAS). — 75, 77. Schunke 14171 (FLAS). — 78. Schunke 14174 (FLAS).

Vernacular names and uses. Cebolla de la selva, sugkip, sacha cebolla. A poultice of the bulbs is used to treat tumors (Lawesson *et al.* 39632).

Additional specimens examined. COLOMBIA. AMAZONAS: confluencia de los ríos Amazonas y Loretoyacu, 12 Apr. 1975, *Cabrera 3336* (COL); Trapecio amazonico, Loretoyacu River, ca. 100 m, Sep. 1946 (fr), *Schultes & Black 8342* (US); same locality as preceding, Oct. 1946, *Schultes & Black 8410* (GH, US). CAQUETA: Morelia, 150 m, 5 Oct. 1941 (fr), *von Sneidern s.n.* (S). CAUCA: Popayan, 25 Jan. 1935, *Killip s.n.* (COL). ECUA-

DOR. MORONA-SANTIAGO: 15 km N of Macas on road to Río Upano, 2°7'S, 78°8'W, 1,250 m, 20 Feb. 1987, *Bohlin et al. 1498* (GB); road Limón–Macas, ca. km 20 from Limón, primary rain forest and rastrojos, 700–900 m, 26 Mar. 1974, *Harling & Andersson 12915* (FLAS, GB). NAPO: Nuevo Rocafuerte, Río Napo, W of Río Yasuni, Laguna Jatuncocha, *Alarcon 106* (QCA); Misahualli, Guacamayos, Puerto Francisco de Orellana, *Alarcon 19509* (QCA); Napo, forest, 6 Oct. 1939, *Asplund 9122* (S); Tena, marshy forest, 21 Oct. 1939, *Asplund 9488* (S); Limoncocha, 300 m, 22 Jan. 1977, *Dodson 6636* (SEL); 45 minute walk by trail from Santa Cecilia up Río Aguarico, ca. 350 m, 28 Mar. 1972 (fr), *Dwyer*

& *MacBryde* 9699 (MO, QCA); Santa Cecilia, rain forest off runway, 340 m, 30 Mar. 1972 (fr), *Dwyer & Simmons* 9743 (MO); Cañon de los Monos, ca. 12 km north of Coca, 250 m, *Harling & Andersson* 11719 (GB); path from Río Bueno to Santa Rosa, *Harling et al.* 7201 (GB); Río Jivino, Limoncocha, 13–15 Mar. 1968, *Harling et al.* 7673 (FLAS, GB); Armenia Vieja at Río Napo, ca. 12 km SW of Coca, 12 Jan. 1973, *Holguer* 2655 (FLAS, GB); Cañon de los Monos, road Coca–Lago Agrio, ca. 12 km north of Coca, 24 Jan. 1973, *Holguer* 2960 (GB); Santa Cecilia, Lago Agrio–Baeza, ca. 16 km west of Lago Agrio, 27 Feb. 1973, *Holguer* 3532 (FLAS, GB); Río Aguarico W of Detacamento Zancudo at entrance of Río Zancudo, 320 m, very rich soil, 29 Aug. 1979 (fr), *Holm-Nielsen et al.* 20168 (AAU); Río Aguarico, Sarayacu, 29 June 1980, *Jaramillo & Coello* 2145 (QCA); Coca, km 15 from road to Las Yucas, 300 m, 31 Jan. 1980, *Jaramillo & Coello* 2191 (QCA); Río Cuyabeno, Puerto Bolivar, 6 July 1980, *Jaramillo & Coello* 2852 (QCA); Dureno, right bank of Río Aguarico, 10 July 1980, *Jaramillo & Coello* 2962 (QCA); Anañgu, Río Napo, 76°23'W, 0°32'S, 260–350 m, 27 June 1983, *Lawesson et al.* 39632 (AAU); 4.2–7.5 km west of Lago Agrio (5–8.2 km east of Río Conejo) near Lago Agrio–Baeza Road, ca. 340 m, 31 Mar. 1972, *MacBryde & Dwyer* 1387 (MO); ex hort., voucher of SEL Acc. 78-1099, collected vicinity Limoncocha, 240 m, 15 Dec. 1982, *Meerow* 1103 (FLAS). PASTAZA: Mera, ca. 1,100 m, 3 Mar. 1956, *Asplund* 19571 (S); 3 km NW of Mera on road from Mera–Río Anzu, Hacienda San Augustin, 900–1,300 m, *Dodson et al.* 15717 (MO); Curaray (Jesús Pitishka), virgin rain forest near the posto militar, ca. 200 m, 18 Mar. 1980, *Harling & Andersson* 17374 (FLAS, GB); between Nalpi and Canelo, 26 Feb. 1971, *Holguer* 1504 (FLAS, GB); trail from Indillama to Canelos, 400 m, occasional, 5 Feb. 1935, *Mexia* 6855 (UC, US); Río Curaray, mouth of Río Querano, 1°30'S, 76°32'W, 230 m, 3 Sep. 1985, *Neill & Palacios* 6828 (MO); 2 km NE of Mera, Hacienda San Antonio del Baron von Humboldt, 1°27'S, 78°6'W, 1,300 m, 27 Feb.–19 Mar. 1985, *Palacios et al.* 75 (MO); Napo road north of Puyo, 16 Feb. 1953, *Prescott* 438 (NY). TUNGURAHUA: valley of Pastaza River, between Baños and Cashurco, 8 hours east of Baños, 1,300–1,800 m, *Hitchcock* 21891 (GH, NY, US); vicinity of Río Margarjitas on Canelos trail, 1,225 m, 19 Mar. 1939, *Penland & Summers* 142 (US). PERU. AMAZONAS: Quebrada Huampami, lugar tseasim, monte al lado nayumpin, 800 ft., 3 Apr. 1973, *Ancuash* 161 (MO); Quebrada de Apigkagentsa, Río Cenepa, 720 ft., *Kayap* 597 (F, MO); Quebrada Cunup, monte cerca a la chacra, 800–850 ft., 24 July 1974 (fr), *Kayap* 1298 (MO); Río Cenepa, vicinity of Huampami, ca. 5 km E of Chavez Valdivia, ca. 78°30'W, 4°30'S, 3 Aug. 1978, *Kujikat* 154 (MO); Río Cenepa, vicinity of Huampami, ca. 5 km east of Chavez Valdivia, ca. 78°30'W, 4°30'S, Quebrada Aintami, 17 Aug. 1978, *Kujikat* 415 (MO). LORETO: Maynas, Yanamono, Explorama Tourist Camp, Río Amazonas, between Indiana and mouth of Río Napo, 72°48'W, 3°28'S, 120 m, 18 Aug. 1980, *Gentry et al.* 29867 (MO); same locality, 130 m, 18 Feb. 1981, *Gentry et al.* 31418 (MO); Maynas, Iquitos, Río Ampiyacu, 4 vueltas de Monona Cocha, 4 Aug. 1976, *Revilla* 990 (MO); Alto Amazonas, Yurimaguas, Camino a “Shunguyco,” al sur-este de Puerto Arturo, cerca a Yurimaguas, 150–200 m, 1 Dec. 1984, *Schunke* 14157 (FLAS). SAN MARTÍN: road between Moyobamba and Chachapoyas near km marker 415, 13.5 km W of Naranjos, 5°38'S,

77°25'W, 700 m, 12 Apr. 1984, *Croat* 58172A (MO); Mariscal Caceres, Tocache Nuevo, Camino a Shunté, 12 Mar. 1970, *Schunke* 3856 (F); Lamas, Alonso de Alvarado, San Juan de Pacaizapa, km 72, carretera Tarapoto–Moyobamba, 1,000–1,050 m, 9 June 1977, *Schunke* 9675 (F); Lamas, Alonso de Alvarado, Fundo Las Malvinas, carretera Moyobamba–Tarapoto, km 43, 850 m, 6 Dec. 1984, *Schunke* 14174 (FLAS); San Roque, in humid loam, 1,350–1,500 m, 5 Feb. 1930, *Williams* 7748 (F).

Eucharis formosa is the most commonly encountered species in eastern Ecuador (Fig. 71). It extends into Amazonian Peru and Colombia and occurs in the lower “ceja de la selva” forests of north-central Peru (Fig. 72). Like the closely related *E. candida*, *E. formosa* has a wide elevational range, possibly in part from cultivation (Meerow, 1987e). The flowers emit a mild and unpleasant “sour” odor. *Eucharis formosa* is larger in all parts than *E. candida* and generally has more ovules per locule. The conspicuous horn on the apiculum of the outer tepal is characteristic of Ecuadorean populations of *E. formosa* (Fig. 67Ai); this character is not obvious in Peruvian collections. Forms with toothed or edentate staminal cups occur throughout the range of this species without any observable geographic pattern (Fig. 70B). Flowers of the same inflorescence can vary for this character. A Peruvian collection (*Schunke* 14174) shows some karyotypic and allozyme divergence from Ecuadorean populations (Meerow, in press). In floral morphology (Fig. 78), however, it is indistinguishable from other Ecuadorean material. A second collection (*Schunke* 14171), from the same general vicinity of Peru as *Schunke* 14174, has only shallowly plicate leaves and reduced pigmentation of the staminal cup (Figs. 76, 77). At present, too little is known about *E. formosa* in Peru to justify recognition of subspecific taxa.

3. *Eucharis bakeriana* N. E. Brown, Gard. Chron. 7: 416, fig. 61. 1890. TYPE: Colombia (?): no other data, ex hort. Sander and Co., 1890, *s.n.*, in part (holotype, K). *Urceolina bakeriana* (N. E. Brown) Traub, Pl. Life 27: 57–59. 1971. Figure 79.

Bulb to ca. 5 cm diam., the tunics brown. Leaves 2–4; petiole 15–17, 25–30 cm long, (5–)10–11 mm wide; lamina elliptic, 24–29.5, 44–55 cm long, (10–)17–20 cm wide, somewhat succulent, smooth. Scape 6–8 dm tall, ca. 1 cm diam. proximally, 5–7 mm diam. distally; bracts ovate-lanceolate, 30–38 mm long, ca. 10 mm wide at the base. Flowers (5–)10, with a mild, sweet fragrance, pedicels 10–30 mm long; tube 35–40 mm long,

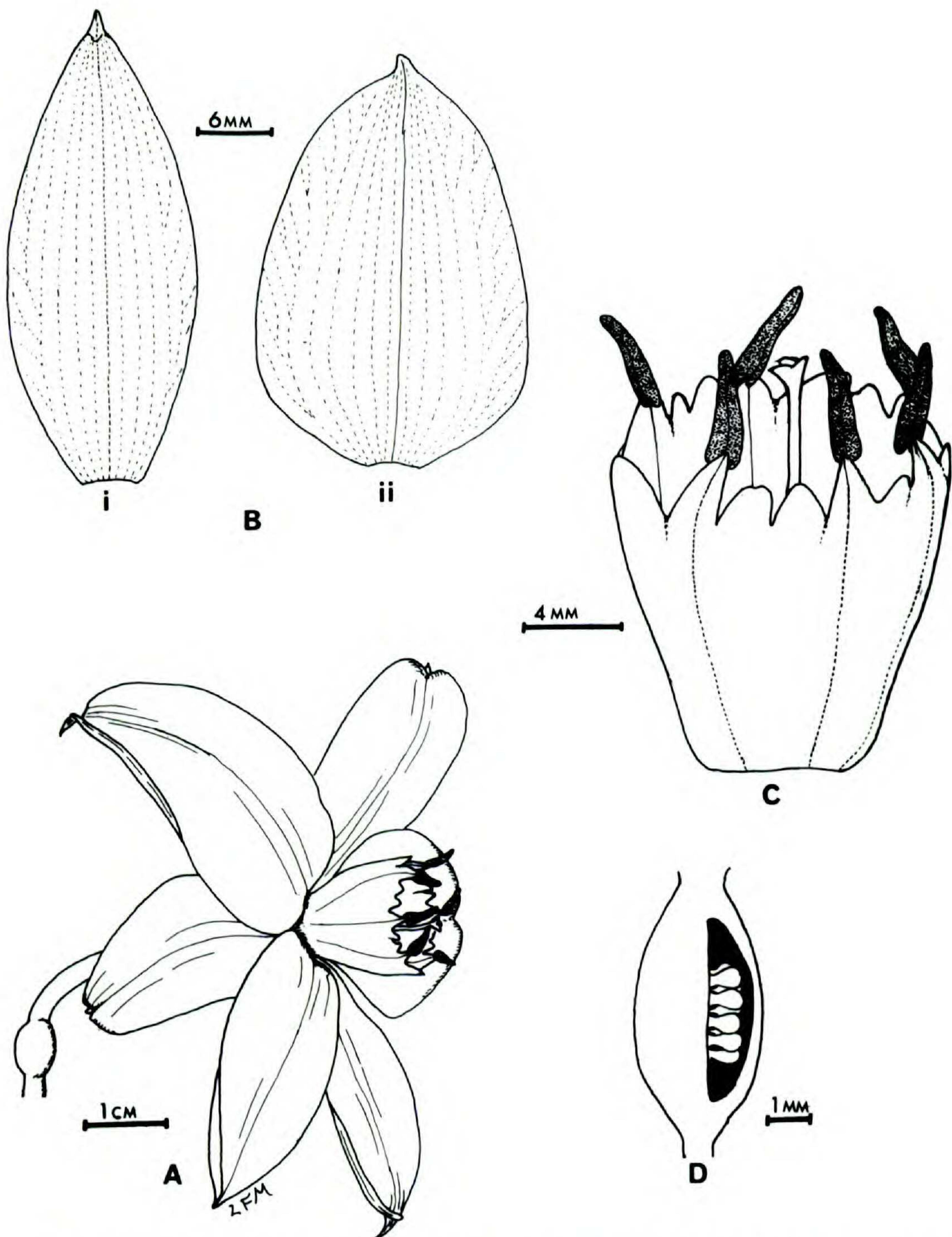


FIGURE 79. *Eucharis bakeriana* (Meerow 1108, FLAS).—A. flower.—B. Tepals. i. Outer tepal. ii. Inner tepal.—C. Staminal cup.—D. Ovary, longitudinal section.

2–3 mm wide for most of its length, abruptly dilated near the throat to 9–9.7 mm wide, curved abruptly just above the ovary and straight for the rest of its length, thus perpendicular to the vertical axis of the scape; limb spreading to 50–60 mm wide; outer tepals 28.5–32 mm long, ca. (10–)16.8 mm wide, ovate-lanceolate to ovate, apiculate; inner tepals 26–30 mm long, (14–)20–22 mm wide, ovate, acute to minutely apiculate. Staminal cup subcylindrical to campanulate, ca. 16 mm long (to apex of teeth), 13–15 mm wide, slightly plicate between the filamental trace, very shallowly cleft between each stamen (< 1 mm), proximally marked green, obtusely bidentate between each free filament; teeth 2–3 mm long, half the length of the subulate portion of the free filament; each stamen

5–6.4 mm wide tooth to tooth; subulate portion of the filament 3–4.5 mm long, 1.5–1.7 mm wide; anthers oblong, 5.4–6 mm long; pollen grain ca. 50.7 μm polar diam., ca. 76.9 μm longest equatorial diam. Style 45–54.5 mm long, exerted just slightly past the anthers; stigma 2.4–2.8 mm wide. Ovary ellipsoid, 6.5–7 mm long, 5.3–6.5 mm diam.; ovules 2–3, 8–9 per locule. Capsule ca. 1.5–2 cm long, 2.5–3 cm wide, bright orange, leathery; seeds ellipsoid, ca. 1 cm long, 0.5 cm diam., with a lustrous, smooth black testa. Chromosome number: $2n = 46$.

Distribution. Very rare in the understory of lower montane rain forest in the middle Río Huallaga valley of Peru, 800 m (Fig. 72). Living material

from which the type specimen was prepared was reportedly collected in Colombia, but I have seen no Colombian material. Flowering season not known.

Additional specimens examined. PERU. SAN MARTÍN: 17 km NE of Tarapoto on road to Yurimaguas, trail along stream to waterfall, wet premontane forest on rocky hills, 6°30'S, 76°20'W, 800 m, 21 July 1982 (fr), *Gentry et al.* 37852 (MO); vicinity of Tarapoto, no other data, flowered in cultivation from material collected by L. Besse, *Meerow 1108* (FLAS).

The type of *E. bakeriana* was prepared from living material supposedly collected in Colombia. When I examined the type specimen, only the several large flowers present in the fragment packet resembled the figure that accompanied Brown's (1890) description of *E. bakeriana*. The mounted material was referable to the smaller-flowered *E. candida*. At the time, I thought that *E. bakeriana* might represent an aberrant form of *E. candida*. Several years later I received a bulb of a *Eucharis* collected near Tarapoto, Peru, by Libby Besse of SEL. The flowers that grew from the bulb bore an exact resemblance in habit and staminal cup morphology to *E. bakeriana*, though with considerably more ovules per locule. At present, *E. bakeriana* is known only from the type, the Besse material, and a fruiting specimen referred to this species on the basis of leaf size.

Eucharis bakeriana is distinct from *E. formosa*, its closest phenetic relative, by its nonpendent flowers that are perpendicular to the vertical axis of the scape, very shallowly cleft staminal cup (< 1 mm, vs. 2 mm in *E. formosa*), short subulate portion of the stamen, and sweet floral fragrance (slightly fetid in *E. formosa*). In leaf size and karyotype, *E. bakeriana* is very similar to Peruvian material of *E. formosa* (*Schunke 14174*) but differs by its greater number of subtelocentric chromosomes and the submetacentric morphology of the second-largest pair (Meerow, 1987b). The leaves are only shallowly, if at all, plicate and are thicker.

4. *Eucharis bonplandii* (Kunth) Traub, Pl. Life 7: 40. 1951. *Hymenocallis bonplandii* Kunth, Enum. Pl. 5: 666. 1850. TYPE: Colombia. Cundinamarca: Río Magdalena, near Nares, *Bonpland 1657* (holotype, P, photo of type, NY). *Caliphruria bonplandii* (Kunth) Baillon, Bull. Mens. Soc. Linn. Paris 143: 1136. 1894. *Urceolina bonplandii* (Kunth) Traub, Pl. Life 27: 57–59. 1971. Figure 80.

Bulb subglobose, 41–46 mm long, 29–32 mm wide, neck ca. 18 mm long and wide, tunics brown. Leaves 2, somewhat succulent; petiole 8–14(–18)

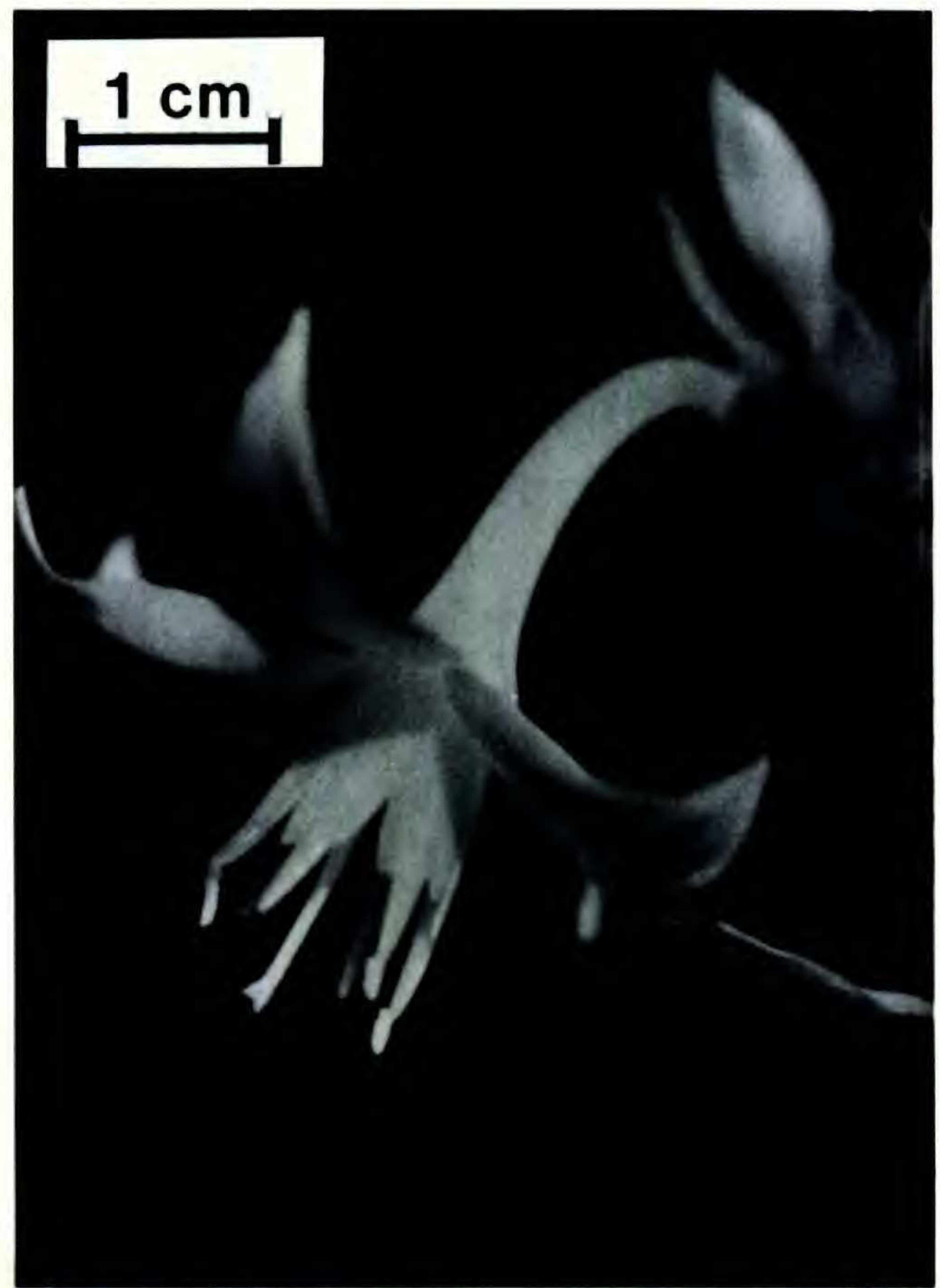


FIGURE 80. *Eucharis bonplandii* (Meerow 1098, FLAS).

cm long, 6–8 mm thick proximally, 3–4 mm distally, always shorter than the lamina; lamina elliptic, (16–)18–24(–26) cm long, 8.5–11.5 cm wide, bluish green, especially in strong light, slightly glaucous adaxially; lighter green abaxially, the abaxial cuticle densely striate; apex acute to shortly acuminate; attenuate at the base. Scape 4.5–5.8 dm tall, 6–8 mm diam. proximally, 3–4 mm diam. distally; bracts (25–)33–40 mm long, ovate-lanceolate, greenish white. Flowers 5–7, nonfragrant, pendent; pedicels 18–25 mm long; tube 25–33 mm long, 1.8–2.5 mm wide for most of its length, abruptly dilated at the throat to 7–9(–10) mm wide; limb spreading to 47–55 mm wide; outer tepals ovate-lanceolate, 25.7–30.5 mm long, 8–10 mm wide, apiculate; inner tepals 23–28 mm long, 11.5–14 mm wide, acute to minutely apiculate. Staminal cup subcylindrical, (11.5–)12.5–14.3 mm long (to apex of teeth), 11.5–13 mm wide, stained pale yellow proximally, irregularly bidentate between each free filament, one stamen occasionally only lobed or quadrate, cleft 2.6–4 mm between each stamen; teeth variously acute or obtuse, 1–2 mm long; each stamen 3.6–4.5 mm wide tooth to tooth; free portion narrowly subulate, (3.8–)4.5–5.8 mm long, ca. 1.8 mm wide; anthers 4–4.8 mm long, oblong, grayish-brown; pollen grain ca. 43.5 μ m polar diam., ca. 63 μ m longest equatorial diam. Style 50–60 mm long, exerted just beyond the

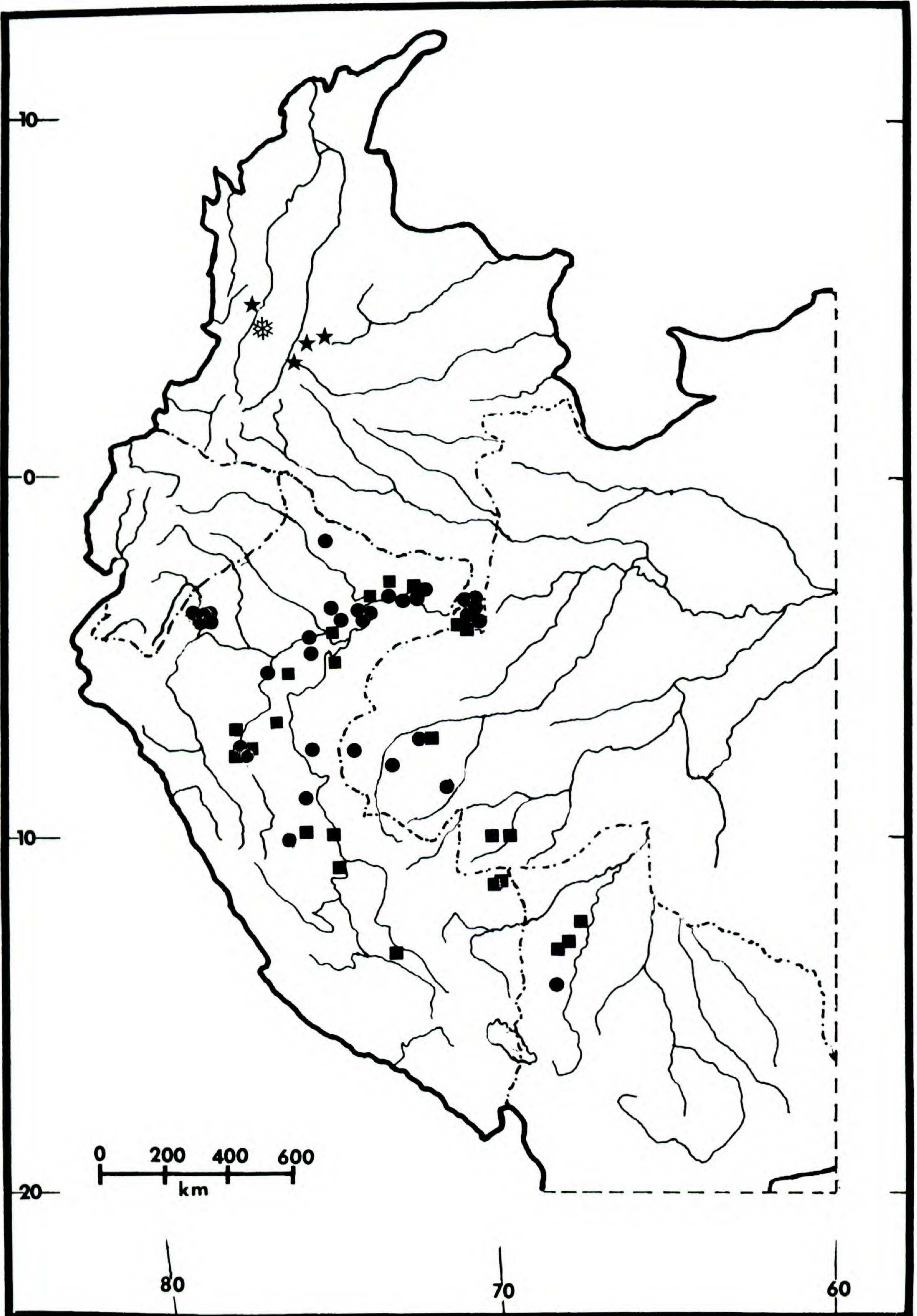


FIGURE 81. Distributions of *Eucharis bonplandii* (stars), *E. caucana* (snowflake), *E. cyaneosperma* (squares) and *E. ulei* (circles) in northwestern-central South America.

anthers; stigma 2–2.7 mm wide. Ovary subglobose, ca. 5–6 mm diam.; ovules 2–3 per locule. Capsule ca. 1 cm long, 2 cm wide, bright orange, leathery; seeds 1–2 per locule, ellipsoid, ca. 1 cm long, ca. 0.5 mm diam., with a lustrous black testa. Chromosome number: $2n = 92$.

Distribution. Rare in central and western Colombia (Fig. 81), in the understory of lower montane rain forest, 400–600(–1,300 m). Flowering February–March, May–June, August.

Additional specimens examined. COLOMBIA. Department unknown: La Mejita (?), June 1844, *Goudot s.n.* (K, P). CALDAS: Cauca Valley, Tabeja, west of Armenia, 1,100–1,300 m, 23 July 1922, *Pennell et al. 8604* (GH, NY, US). CUNDINAMARCA: Viotá, Quebrada Cachinibulo, 550 m, 18 Feb. 1876, *Andre 1583* (K); same locality as preceding, 600 m, 19 Feb. 1876, *Andre 1721* (K); ex hort. originally collected by J. Paxton near Bogotá, ca. 650 m, received from Foster Gardens, Hawaii, 14 May 1982, *Meerow 1098* (FLAS). TOLIMA: valle del Alto Magdalena, vereda La Chamba (municipio del Guamo), 400 m, 3 Mar. 1963 (fr), *Uribe 4218* (COL).

Eucharis bonplandii is one of only two tetraploid ($2n = 92$) species so far known in the genus. The species is known only from Colombia, and has been rarely collected. Among Amazonian species, *E. bonplandii* has the greatest phenetic relationship to *E. ulei*, with five similarly sized flowers and two ovules per locule in common. It may be separated from *E. ulei* by having succulent, glaucous leaves and short petioles. The staminal cup of *E. bonplandii* is pigmented pale yellow at its base; that of *E. ulei* is marked green. *Eucharis bonplandii* and *E. bouchei* are the northernmost species of subg. *Eucharis*, and thus may form a monophyletic, tetraploid group (Meerow, 1987d). Both species have relatively short petioles. From *E. bouchei*, *E. bonplandii* differs primarily by its leaf glaucousness and longer pedicels.

5. ***Eucharis bouchei*** Woodson & Allen, Ann. Missouri Bot. Gard. 24: 181. 1937. *Urceolina bouchei* (Woodson & Allen) Traub, Pl. Life 27: 57–59. 1971. TYPE: Panama. Coclé: El Valle de Antón, 500–700 m, 23–27 July 1935, *Seibert 466* (holotype, MO). Figure 82.

Bulb subglobose, 30–45(–85) mm long, (25–)30–40(–50) mm diam.; neck short, to 25 mm long, 10–20 mm wide; tunics brown. Leaves 1–3 (–4); petiole (9–)15–25(–28) cm long, 7–8 mm wide proximally, 5–6 mm wide distally; lamina widely (ovate-)elliptic, (17–)20–25(–40) cm long, (7–)8–10(–14) cm wide, shortly acuminate, slightly succulent, lustrous bright green adaxially, dull

pale green abaxially, smooth, margins mostly non-undulate; abaxial cuticle largely devoid of striation. Scape ca. (4–)5.5 dm tall, ca. 1 cm diam. proximally, ca. 5 mm diam. distally; bracts ovate-lanceolate, 25–36(–47) mm long, (5–)7–10 mm wide at the base. Flowers (3–)5(–6); usually pendent, sometimes only declinate, not fragrant; pedicels 5–10(–20) mm long, very rarely less than 5 mm; tube (25–)33–45 mm long, cylindrical and (1.5–)2–2.5(–3) mm for most of its length, abruptly dilated near the throat to (7–)8–10(–12) mm wide, usually curved gradually, but sometimes only curved abruptly at the base, in which case nearly straight for most of its length; tepals spreading widely from the throat (ca. 90°) or sometimes only at an angle of 45–60°; outer tepals ovate-lanceolate, (18–)21–28(–32) mm long, 8–11(–15) mm wide, apiculate; inner tepals ovate, (16–)20–26(–32) mm long, (10–)12–15(–17) mm wide, obtuse to acute. Staminal cup subcylindrical, 9–12(–15) mm long to apex of filament, (10–)12–15(–18) mm wide, deeply cleft between each stamen to 3–5 mm, usually edentate but variably lobed, acutely or obtusely bidentate, or irregularly toothed between each stamen, marked pale green to greenish yellow proximally; each stamen (3.5–)4–5 mm wide at the base, 4–6(–7) mm long, either trapezoidal in shape (in which case dilating gradually from apex to base), or abruptly dilated at $\frac{1}{2}$ – $\frac{1}{4}$ of its length (in which case the upper portion narrowly subulate and 2–3 or 3–4 mm long, 1.5–2 mm wide); anthers oblong, 3.5–4.5 mm long; pollen grain 45.7–49.65 μm polar diam., 66.8–68.43 μm longest equatorial diam. Style (30–)45–60 mm long, exerted 0.5–1 cm beyond anthers; stigma 2–3 mm wide. Ovary globose or ellipsoid and deeply trigonous, rarely not trigonous, 5–8 mm long, 4–6(–6.5) mm diam., usually wider than long when deeply trigonous; ovules 2–3(–4, very rarely 5) per locule, superposed in the lower half of the cell. Capsule 1.5–2 cm long, 2–3 cm wide, bright orange, leathery; pedicels 15–27 mm long; seeds 1–2 per locule, ellipsoid, ca. 1 cm long, 0.5 cm diam., with a lustrous, smooth, black testa. Chromosome number: $2n = 92$.

KEY TO THE VARIETIES OF *E. BOUCHEI*

- 1a. Staminal cup edentate, or occasionally with one obscure tooth at the base of one stamen; stamens trapezoidal and gradually dilated from apex to base or, if obscurely constricted distally, subulate portion more than 2 mm wide; Coclé and Colón provinces of Panama, rare in Panamá Province and in Costa Rica and Guatemala
..... 5a. *E. bouchei* var. *bouchei*
- 1b. Staminal cup lobed or toothed; stamens abruptly

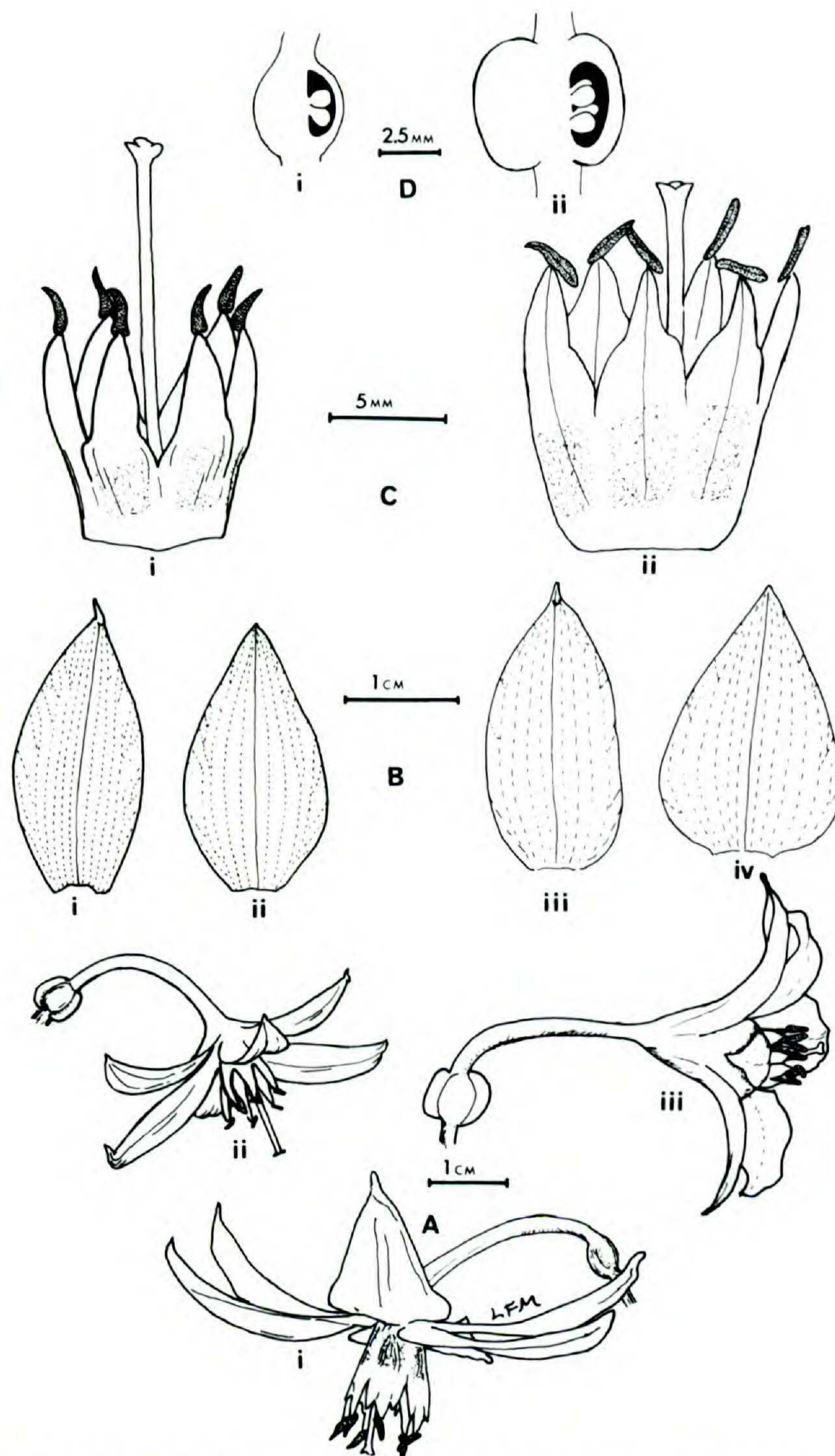


FIGURE 82. *Eucharis bouchei*. — A. Flowers. i. Variety *dressleri* (holotype, Meerow 1107, FLAS). ii, iii. Variety *bouchei*. ii, Meerow 1125 (FLAS); iii, Meerow 1157 (FLAS). — B. Tepals, variety *bouchei*. i, ii. Meerow 1125. i, outer tepal; ii, inner tepal. iii, iv. Meerow 1157. iii, outer tepal; iv, inner tepal. — C. Staminal cups, variety *bouchei*. i, Meerow 1125; ii, Meerow 1157. — D. Ovaries, variety *bouchei*, longitudinal section. i, Meerow 1125; ii, Meerow 1157.

constricted distally at $\frac{1}{2}$ – $\frac{1}{4}$ length into a subulate portion 1.5–2 mm wide 2

2a. Outer tepals 26–32 mm long; staminal cup irregularly toothed, the teeth acute; subulate portion of filament 3.5–4.5 mm long; ovary not deeply trigonous; ovules 2–4 per locule; Coclé Province of Panama near El Valle 5b. *E. bouchei* var. *dressleri*

2b. Outer tepals 20–26 mm long; staminal cup obtusely bidentate or lobed; subulate portion of filament up to 3.5 mm long; ovary deeply trigonous; ovules 2–5 per locule; Panamá and Darién provinces of Panama, rare in Guatemala

..... 5c. *E. bouchei* var. *dariensis*

5a. *Eucharis bouchei* var. *bouchei*. Figures 70Ci–ii, 82Aii–iii, B.

Perianth tube (30.8–)34–45 mm long; outer tepals (18–)24–28(–35) mm long, (8.8–)9.4–15.5 mm wide; inner tepals 21–26(–31) mm long, 11–17.5 mm wide. Staminal cup (8, 9–)11.5–15(–16.7) mm long (to apex of filaments), (9–)12–15.5(–16, 18) mm wide, edentate or rarely with a single obscure tooth between one or several stamens; each stamen trapezoidal in shape, dilating gradually from apex to base, or, if obscurely constricted in the distal 2–3 mm, then the subulate

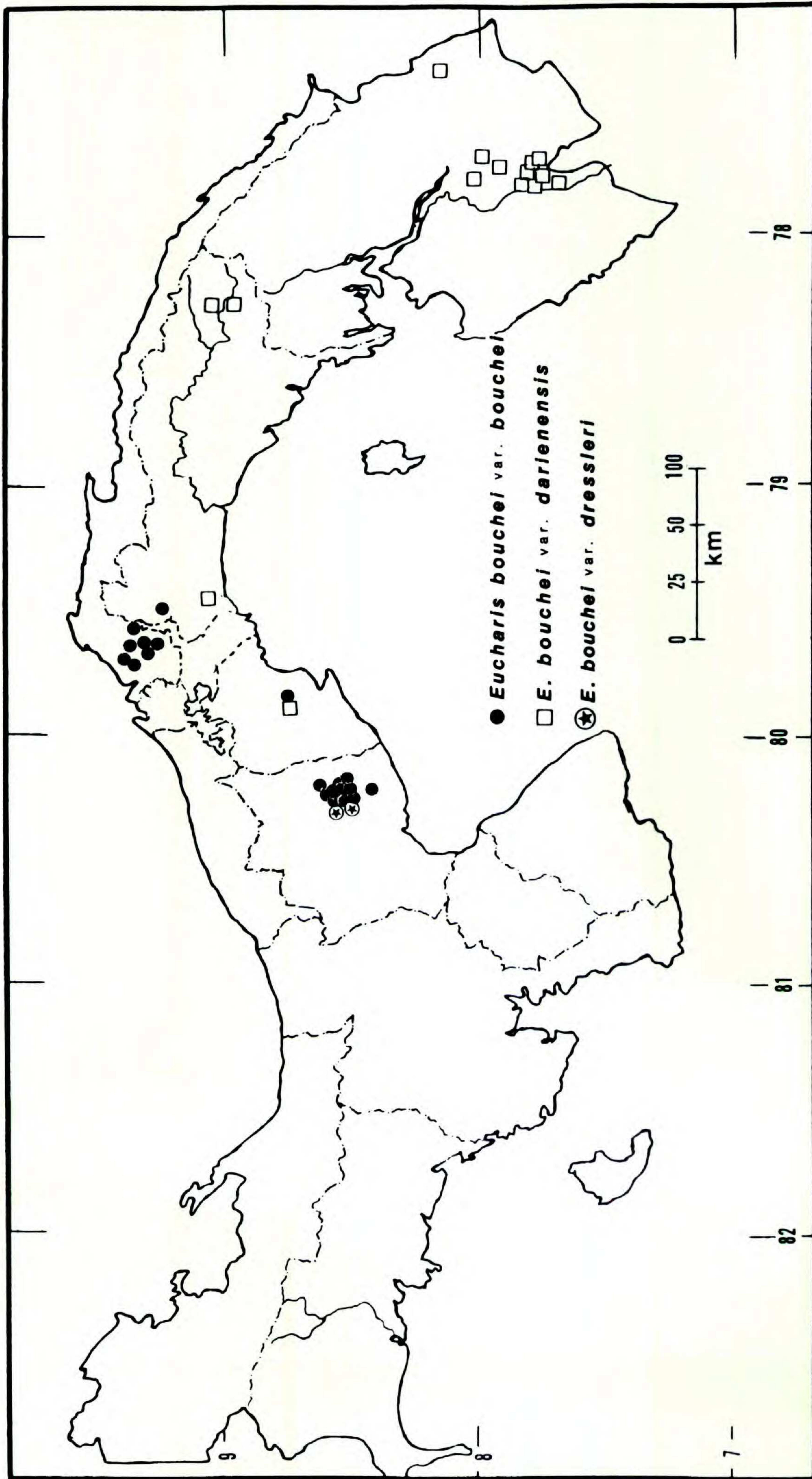


FIGURE 83. Distribution of *Eucharis bouchei* in Panama.

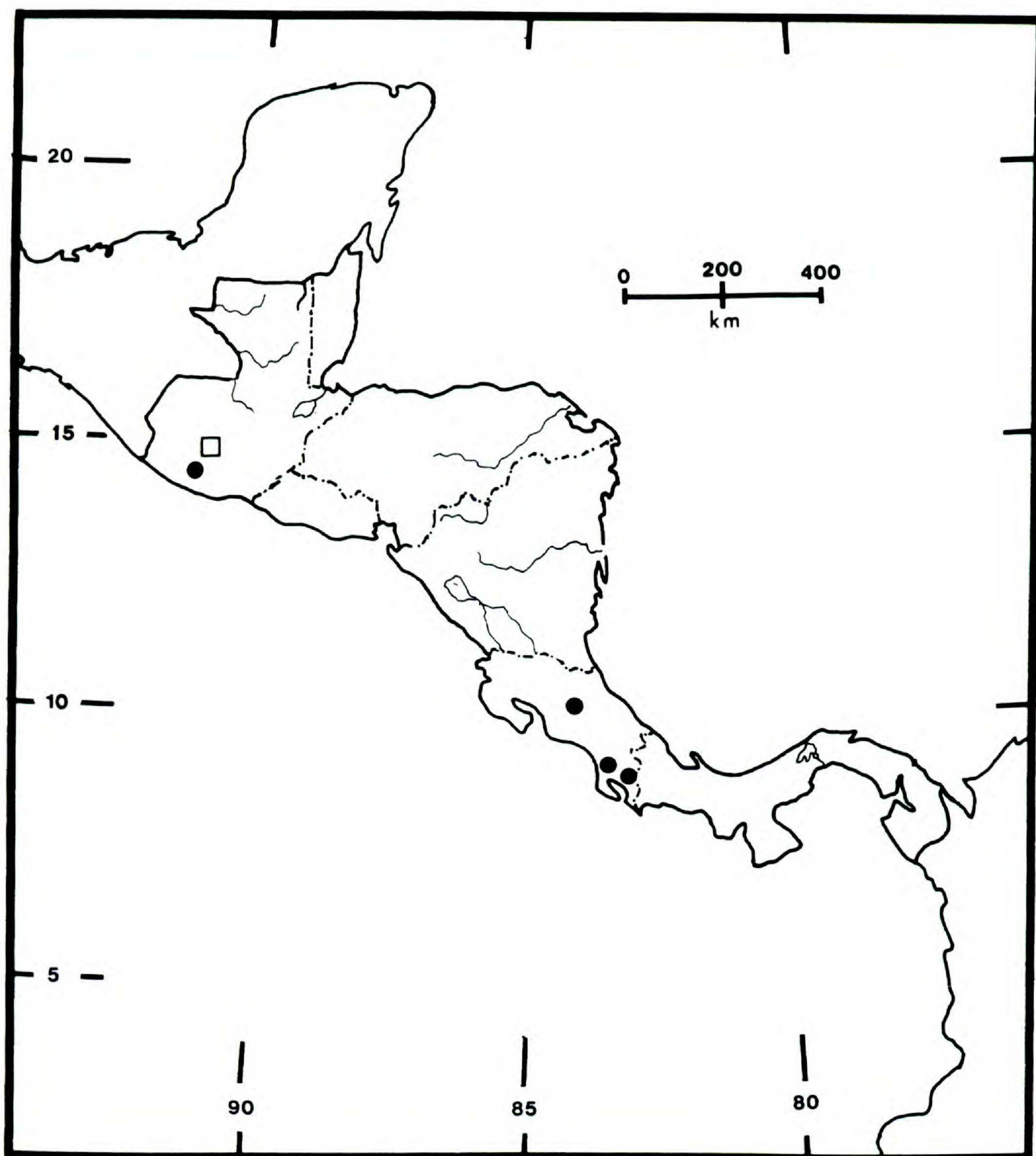


FIGURE 84. Distribution of *Eucharis bouchei* in Central America exclusive of Panama. Circles = *Eucharis bouchei* var. *bouchei*; square = *E. bouchei* var. *darienensis*.

portion wider than 2 mm. Style exerted ca. 1 cm beyond the anthers. Ovary trigonous; ovules 2–3(–4) per locule.

Distribution. Understory of primary, pre-montane and lower montane rain forest in Coclé and Colón provinces of Panama (Fig. 83), particularly in the vicinity of El Valle de Antón and the Río Guancho valley; rare in Panamá Province, Costa Rica, and Guatemala (Fig. 84); frequently

on steep slopes; (200–)500–1,000 m. Flowering (March) June–August, October–December.

Additional specimens examined. COSTA RICA. PUNTARENAS: Canton de Osa, hills near Palmar Norte, Río Grande de Terraba, 2,000 ft., Allen 5347 (F, K, MO, US); cataratas de San Ramón, 26 Feb. 1931, Brenes 13515 (F). SAN JOSÉ: El Rodeo, Mar. 1931, Lankester s.n. (F). GUATEMALA. SUCHITEPEQUEZ: Finca Moca, steep, bushy slope, 3,300 ft., 31 Oct. 1934, Skutch 1585 (F). PANAMA. COCLÉ: lower Río Antón, vic. El Valle de Antón, 800–1,000 m, 30 Dec. 1936, Allen 120 (GH, MO); vic.

of El Valle de Antón, 600–1,000 m, *Allen 1228* (GH, MO); vic. El Valle de Antón, ca. 600 m, 10 Dec. 1939, *Allen 2063* (MO); hills north of El Valle de Antón, 100 m, 14 Aug. 1940, *Allen 2182* (MO); region north of El Valle de Antón, ca. 1,000 m, 21 Aug. 1946, *Allen 3641* (G); La Mesa, above El Valle, 600–800 m, 18 Jan. 1968 (fr), *Duke & Dwyer 15180* (NY); 1–3 mi. W of Portobello, *Gentry 1750* (MO); foot of Cerro Pilón, 11 Jan. 1972 (fr), *Gentry & Dwyer 3634* (F, MO); foot of Cerro Pilón, 11 Jan. 1972 (fr), *Gentry & Dwyer 3636* (MO); El Valle de Antón, along Río Indio Trail, 500–700 m, (fr), *Hunter & Allen 338* (G, MO, P, US); el Valle de Antón, 1,000–2,000 ft., edge of cloud forest and roadside, Dec. 1967, *Lewis et al. 2617* (MO); ex hort. from bulb collected by M. Whitten & M. Elliot, vic. El Valle, flowered in cultivation, 25 July 1984, *Meerow 1125* (FLAS); Cerro Pilón, 5 km north of El Valle, 800–1,045 m, 13 June 1975, *Mori et al. 6586* (AAU); Quebrada Amarillo, north of El Valle, 17 Oct. 1975, *Witherspoon & Witherspoon 8736* (MO). COLÓN: Río Guanache, 16 Nov. 1975, *D'Arcy 9679* (MO); hills just north of Río Guanache, 1–200 m, 16 Nov. 1975 (fr), *Davidse & D'Arcy 10096* (MO); Cerro Brujo, ex hort., collected by R. Dressler, flowered in cultivation, July 1985, *Meerow 1157* (FLAS); trail south of Río Guanache, on ridge to Cerro Pan de Azucar, 200 m, *Mori & Kallunki 2014* (AAU); Río Guanache, 6 Nov. 1974 (fr), *Mori & Kallunki 3019* (AAU). PANAMÁ: mountains above Torti Arriba, 2 Dec. 1977, *Folsom et al. 6582* (AAU, BM, MO); near Cerro Campana, on trails radiating from end of road which passes Campana water tank, 23 Aug. 1967, *Kirkbride & Hayden 305* (MO, NY).

5b. *Eucharis bouchei* var. *dressleri* Meerow, var. nov. TYPE: Panama. Coclé: El Valle de Antón, from bulbs collected by R. Dressler in Panama, flowered in cultivation, 17 Mar. 1983, *Meerow 1107* (holotype, FLAS). Figure 82Ai.

Varietas haec ab varietas typica differt staminibus acute dentatis ad 1.5–2.7 mm distale constrictis, ovario non trigono, et ovulis in quoque loculo aliquando plurimioribus.

Perianth tube 30–41 mm long; outer tepals 26.2–32 mm long, 6–10 mm wide; inner tepals 24–28 mm long, 9–13.5 mm wide. Staminal cup 10–16 mm long (to apex of filaments), 9.5–11.5 mm wide, irregularly toothed (some stamens lobed or quadrate), the teeth acute and 1.5–2.7 mm long; each stamen distally constricted abruptly at $\frac{1}{2}$ length, the subulate portion 3.5–4.5 mm long, ca. 1.8 mm wide. Style exerted ca. 0.5 cm beyond the anthers. Ovary not trigonous; ovules 2–4 per locule.

This variety is named in honor of Robert L. Dressler, well-known tropical biologist.

Distribution. Rare rain forest understory herb in Coclé Province of Panama (Fig. 83), in the vicinity of El Valle de Antón, ca. 900 m. Flowering in June.

Additional specimens examined. PANAMA. COCLÉ: El Valle de Antón, 900 m, 4 June 1939, *Alston 8727* (BM).

5c. *Eucharis bouchei* var. *dariensis* Meerow, var. nov. TYPE: Panama. Darién: valley between Cerro Pirre and next most southerly peak, July 1977, *Folsom 4402* (holotype, MO). Figure 70Civ.

Varietas a *Eucharis bouchei* var. *dressleri* affinis sed differt staminibus obtuse dentatis vel lobis et parte staminea distale subulata brevior.

Perianth tube 25.5–36(–43.4) mm long; outer tepals 20–26 mm long, 8–11 mm wide; inner tepals 10.5–24 mm long, (11–)12–15(–16.5) mm wide. Staminal cup 9–10(–13, 16) mm long (to apex of filaments), 12–14.5(–18) mm wide, obtusely bidentate or lobed, the teeth when present ca. 1–1.5 mm long; each stamen distally constricted abruptly at $\frac{1}{2}$ – $\frac{1}{4}$ length; the subulate portion ca. 1.7–3 mm long, 1.5–2 mm wide. Style exerted less than 0.5 cm beyond the anthers. Ovary trigonous; ovules 2–5 per locule.

The varietal epithet refers to Darién Province of Panama, where *E. bouchei* var. *dariensis* is most frequently collected.

Distribution. Understory of primary rain forest in Darién Province of Panama (Fig. 83); rare in Panamá Province and in Guatemala (Fig. 84); 480–1,450 m. Flowering January–February and June–August(–November).

Additional specimens examined. GUATEMALA. SOLOLA: between St. Pedro and Sta. Lucia, 20 Jan. 1857, *Wendland 207* (GOET). PANAMA. DARIÉN: La Boca de Pirre, 13 Oct. 1967 (fr), *Bristan 1285* (MO); vicinity of airstrip at Cana gold mine, 480 m, disturbed forest, 29 July 1976, *Croat 37956* (AAU); Cerro Pirre, cloud forest and/or mossy forest, 2,500–4,500 ft., Aug. 1967, *Duke & Elias 3661* (GH, MO, US); Cerro Tacarcuna, south slope, 1,250–1,450 m, 26 Jan. 1975, *Gentry & Mori 13945* (MO); 0–2 mi. E of Tres Bocas, along shortest headwaters of Río Cuasi, premontane rain forest, 28 Mar. 1968 (fr), *Kirkbride & Duke 1175* (MO); vicinity Cana, 1,750 ft., rare on forest floor, 23 June 1959, *Stern et al. 499* (GH); gold mine at Cana, 480 m, 26 July 1976 (fr), *Sullivan 626* (MO); trail northwest of Cana, 600 m, 28 July 1976 (fr), *Sullivan 718* (MO); gold mine at Cana, 480 m, 29 July 1976 (fr), *Sullivan 753* (MO); Cana–Cuasi trail, Chepigano, 2,000 ft., 12 Mar. 1940 (fr), *Terry & Terry 1533* (F). PANAMÁ: stream flowing out of Serranía de Maje, 10 Feb. 1977 (fr), *Folsom & Collins 1725* (MO); Maje, 5 mi. up Río Maje, steep forested ridge above Chocó Indian trail, 400 m, 19 Nov. 1970, *Kennedy 680* (MO, US); woods around La Eneida, 1,000 m, 5 Aug. 1970 (fr), *Luteyn & Kennedy 1761* (F); lower slopes and trail to Cerro Campana, 13 Sep. 1975, *Witherspoon & Witherspoon 8372* (MO).

Eucharis bouchei is the northernmost species of *Eucharis*, and the only species found north of the Darién Gap. It is also the most variable species in the genus, in characteristics that elsewhere justify specific delimitation. Patterns of variation in floral size and tube and limb habit form a complete mosaic throughout the range of *E. bouchei* that shows little or no geographic consistency (Meerow, 1987d). Staminal cup morphology (Fig. 70C) does, however, demonstrate a fair degree of geographical consistency, and it is chiefly on this basis that I have recognized var. *bouchei* and var. *dariensis*. Variety *dressleri*, rarely encountered mixed with var. *bouchei*, presents a special case, discussed below.

Variety *bouchei*, most common around El Valle de Antón in Coclé Province, is recognized by its largely edentate staminal cup in which the trapezoidal free filament is not markedly constricted distally into a narrow subulate portion (Figs. 70Ci, ii, 82C). The staminal cup of variety *dariensis*, found both in Panamá and Darién provinces, is obtusely bidentate or lobed (Fig. 70Civ). The free filament constricts distally into a narrow (< 2 mm) subulate portion. These two varieties occur in close proximity in one location, near Cerro Campana in Panamá Province (Fig. 83).

The rare var. *dressleri* (Fig. 82Ai), with its acutely toothed staminal cup (Fig. 70Ciii) and shallowly trigonous ovary, occurs close to populations of var. *bouchei*, which is an unstable tetraploid, producing at least some cells with diploid ($2n = 46$) chromosome number (Meerow, 1987d). This variety also does not express either heterozygous or additive banding phenotypes for isozymes of aspartate amino transferase, which otherwise characterizes electrophoretic phenotypes of *E. bouchei* (Meerow, 1987d).

The unprecedented degree of variation in *E. bouchei* is likely the result of two main factors: (1) the species is tetraploid, and (2) it probably represents a geologically recent colonization of Central America by this primarily northern Andean and Amazonian genus (Meerow, 1987d).

Northwesternmost populations representing var. *bouchei* have the most derived androecial morphology (Fig. 70Ci, ii) relative to southeasterly populations (var. *dariensis*, Fig. 70Civ). The latter have staminal cups similar to the generalized morphology characteristic of Andean and Amazonian species of subg. *Eucharis*. This suggests that general movement of *E. bouchei* in Central America has been away from the Colombian border. The occasional presence of *E. bouchei* in Costa Rica is not surprising, but the two reported collec-

tions from Guatemala (*Wendland 207* and *Skutch 1585*) represent a substantial disjunction, or two disjunctions, since the two collections represent different varieties. Given the history of cultivation of Amazonian *Eucharis* by Indian people for medicinal, ceremonial, and possibly ornamental use, the same may have held true in Central America.

6. *Eucharis astrophiala* (Ravenna) Ravenna, *Phytologia* 57: 95–96. 1985. *Urceolina astrophiala* Ravenna, *Pl. Life* 38: 49. 1982. TYPE: Ecuador. Cotopaxi: Quevedo–Latacunga road, km 46 from Quevedo, 79°11'W, 0°55'S, 600 m, 4 Apr. 1973, *Holm-Nielsen et al.* 2851 (holotype not seen, AAU; isotype, S). Figure 85.

Bulb globose, 4–5 cm long, 3–4 cm wide, usually without an appreciable neck, tunics tannish brown. Leaves 2–4 at anthesis, elliptic- or ovate-lanceolate; petiole 10–20 cm long, 4–5.5 mm thick; lamina 15–25 cm long, 5–10 cm wide, thin, non-lustrous, deeply plicate and pustulate, adaxial surface light green, the white midrib conspicuous; abaxial surface whitish green; margin slightly undulate; apically acuminate; basally attenuate to the petiole. Scape 3–4(–5) dm tall, ca. 5 mm diam.; bracts 29–35(–40) mm long, lanceolate. Flowers 5–8(–10); pedicels 8–14 mm long; tube 28–35 mm long, ca. 2 mm wide for most of its length, dilating to (4–)5–6 mm at the throat, strongly curved; perianth limb spreading to 4–5 cm wide; outer tepals 25–30 mm long, (7–)10 mm wide, lanceolate, apiculate; inner tepals 25–28 mm long, 10–12(–14) mm wide, ovate-lanceolate to ovate, acute. Staminal cup funnellform-cylindrical, (10–)12–14 mm long, 8–12 mm wide, edentate, stained orange-yellow basally, cleft between each stamen for $\frac{1}{2}$ – $\frac{2}{3}$ of its length; each free filament (5–)6.4–6.9 mm long, ca. (2.5–)3.5–4.5 mm wide at the base, deltoid; anthers oblong, 5–5.5 mm long; average pollen grain 58.6–60.6 μ m polar diam., 83.0–86.1 μ m longest equatorial diam. Style 50–55 mm long, exerted 5–10 mm beyond the staminal cup; stigma 3-lobed, ca. 2 mm wide. Ovary globose-trigonous, 3.9–4.5 mm long, 3.2–4 mm wide, white at anthesis; ovules 2–3(–4) per locule, medially superposed. Capsule ca. 1–1.5 cm long, 2–2.5 cm wide, bright orange, leathery; seeds 1–2 per locule, ellipsoid, ca. 1 cm long, 0.5 cm diam., with a lustrous, smooth black testa. Chromosome number: $2n = 46$.

Distribution. Endemic to the western declivity of the Andes in north-central Ecuador (Fig. 86), particularly in contiguous areas of Cotopaxi, Los

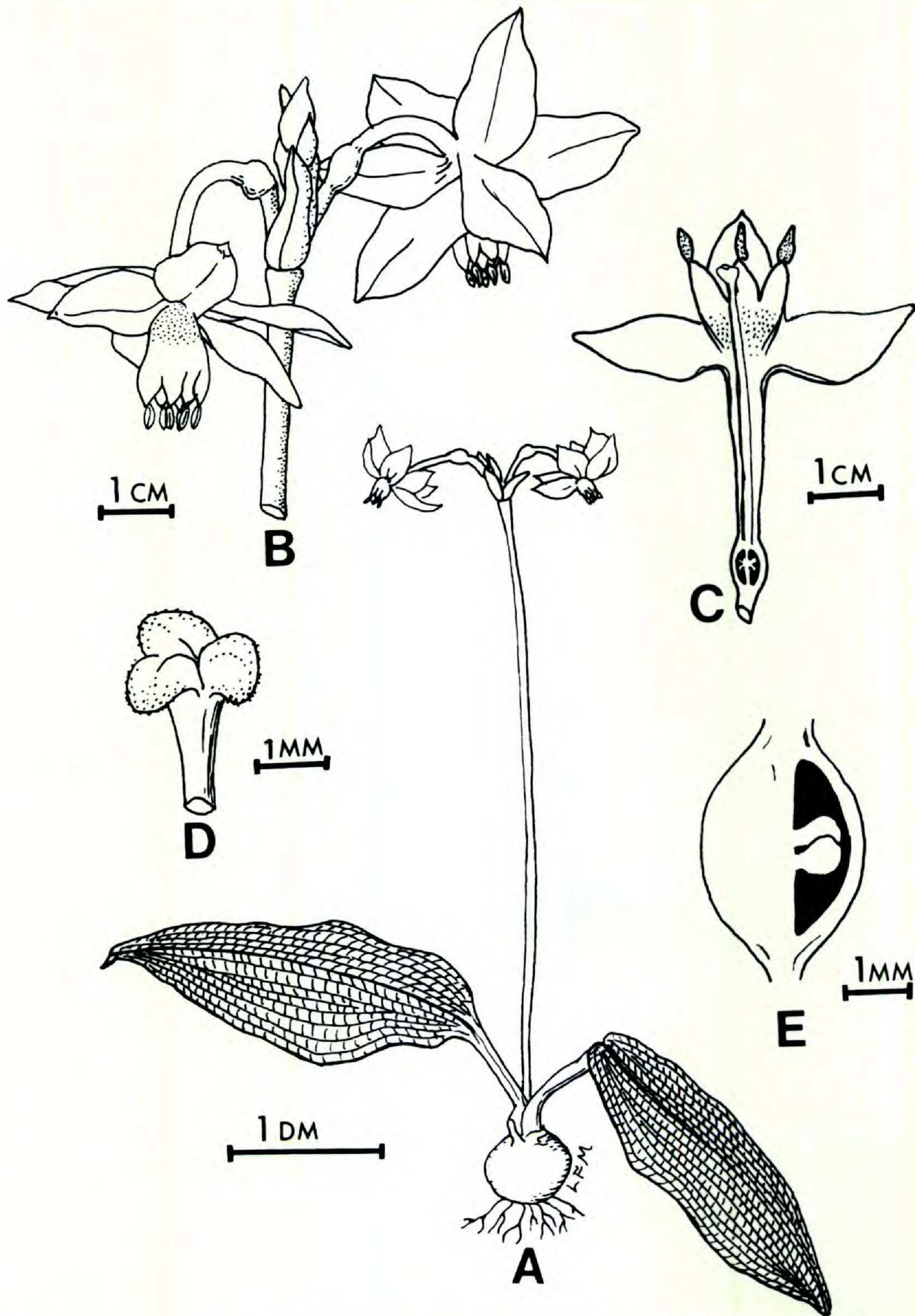


FIGURE 85. *Eucharis astrophiala*, adapted from a drawing by Boots N. Culbertson of Dodson *et al.* 7122 (SEL).—A. Habit.—B. Inflorescence.—C. Flower, longitudinal section.—D. Stigma.—E. Ovary, longitudinal section.

Ríos, and Pichincha provinces, occupying the understory of lower montane rain forest (250–)400–800(–1,100) m elevation. Sporadic flowering may occur at any time but is concentrated in the wetter months of the year.

Additional specimens examined. ECUADOR. BOLÍVAR: Limón, 800–1,100 m, 14 Oct. 1943, *Acosta-Solís* 6374 (F). CHIMBORAZO: km 52–53 on Quevedo–Latacunga road, Tenefuerste, Río Pilalo, Tenefuerste, 750 m, 21 Feb. 1982, *Dodson & Gentry* 12815 (MO, SEL); same locality as *Dodson & Gentry* 10187, 23 May 1983, *Dodson & Gentry* 13793 (MO, SEL); Puente de Chimbo, 250 m, June 1876, *Lehmann* 7775 (K). COTOPAXI: km

40 on road from Quevedo to Latacunga, 600 m, 6 Mar. 1975, *Dodson* 5864 (MO, SEL, US); 3 km E of El Palmar on Quevedo–Latacunga rd., 800 m, 5 Apr. 1980, *Dodson & Gentry* 10187 (MO, SEL); same locality as *Dodson & Gentry* 12815, 750 m, sterile, 15 Aug. 1984, *Meerow & Meerow* 1140 (FLAS). LOS RÍOS: forested hills 12 km east of Patricia Pilar, 650 m, 9 Apr. 1977, *Madison* 3792 (NY). PICHINCHA: Carretera Quito–Puerto Quito, km 113, 00°05'N, 79°02'W, 10 km al norte de la carretera principal, 800 m, 27–29 Dec. 1983, *Balslev & Balseca* 4695 (NY, QCA); same locality, 28 Feb. 1984, *Bravo E.* 417 (QCA); Centinela, Canton Santo Domingo, km 12 E of Patricia Pilar, 600 m, 17 Aug. 1978, *Dodson et al.* 7122 (MO, SEL); 2 km SE of Santo Domingo de los Colorados along Río Verde, 530 m, 5 Feb. 1979,

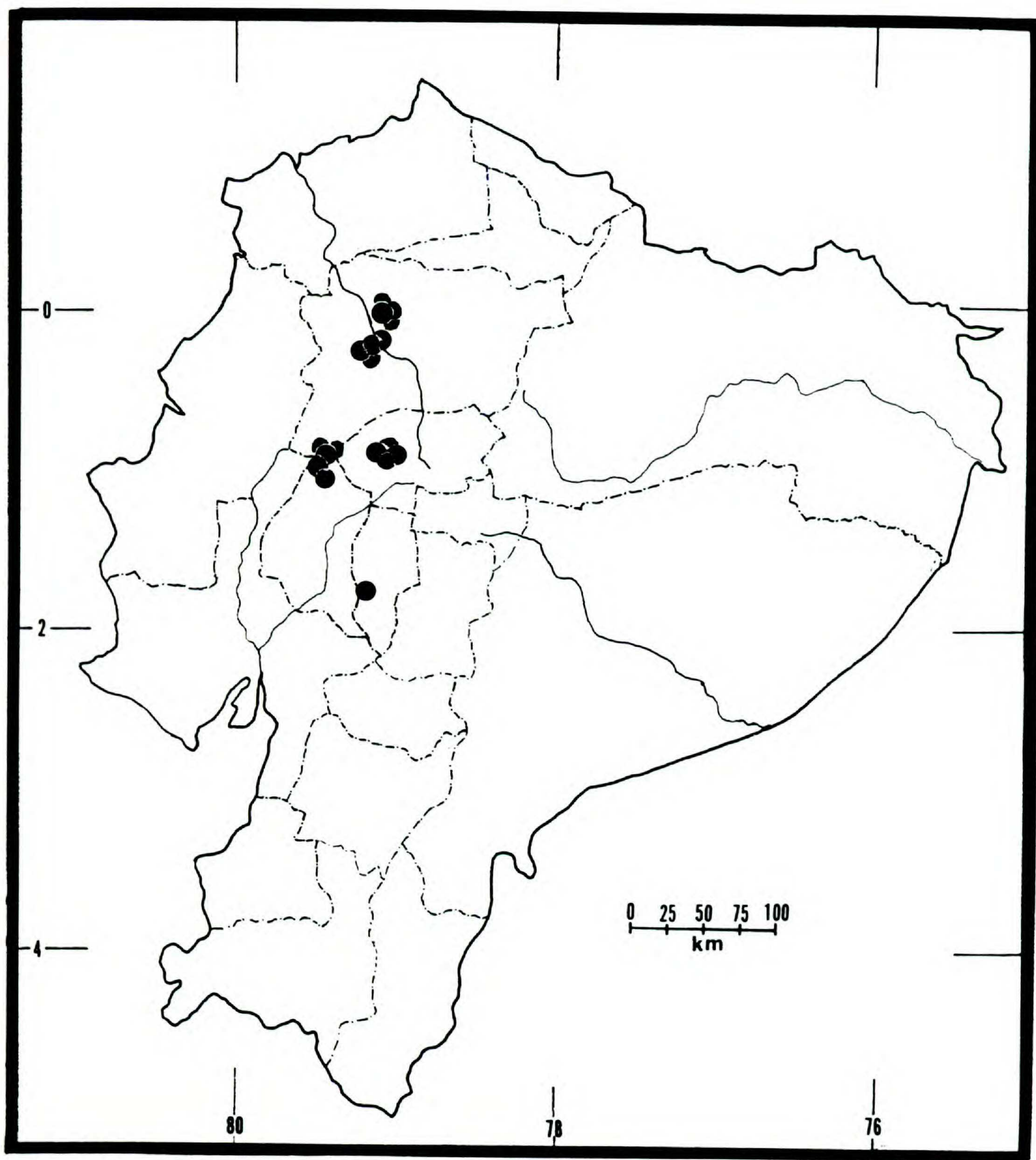


FIGURE 86. Distribution of *Eucharis astrophiala* in Ecuador.

Dodson & Duke 7714 (MO, SEL); road from Patricia Pilar to 24 de Mayo at km 12, path following ridge line at El Centinela at crest of Montañas de Ila, 600 m, 6 Apr. 1980, *Dodson & Gentry 10298* (MO, SEL); Centinela, km 12 on road from Patricia Pilar to 24 de Mayo, km 47 Santo Domingo-Quevedo, 650 m, 30 July 1984, *Dodson et al. 14666* (MO); Centinela, 12 km W of Patricia Pilar, km 45 Santo Domingo-Quevedo, 600 m, 2 Feb. 1985, *Dodson & Neill 15532* (MO); Reserva Endesa, ca. 6 km WNW of P. Vicente Maldonado, mature rain forest, ca. 800 m, 24 Mar. 1985, *Harling & Andersson 23279* (GB); Reserva Forestal Endesa, Río Silanche, km 113 Quito-Puerto Quito, 10 km N of main highway, 0°5'N, 79°2'W, 650-700 m, 25 Feb. 1984,

Jaramillo 6439 (GB); Endesa, km 113 Quito-Puerto Quito, 750 m, 23-24 Apr. 1983, *Rodriguez et al. 91, 92 & 93* (QCA); Santo Domingo de los Colorados, Rancho Brahman, ca. 10 km NW of the town on road to Esmeraldas, 400 m, 31 Mar. 1967, *Sparre 15216* (S).

Eucharis astrophiala is easily separated from the other small-flowered species of subg. *Eucharis* by its uniquely bullate-pustulate and nonlustrous ovate-lanceolate leaves; edentate and deeply cleft staminal cup with deltoid free filaments (Fig. 85B, C); and the second-largest pollen grain in the genus (the largest is that of *E. caucana*). The largest



FIGURES 87, 88.—87. *Eucharis caucana* (type collection).—88. Root-tip mitotic metaphase chromosome configuration of *E. caucana* ($2n = 138$, type collection). Thirteen chromosomes are out of the figure frame.

chromosome pair of *E. astrophiala* is submetacentric, unlike the metacentric pair of all other species of the genus I have examined (Meerow, 1987b). It is the only species of the subgenus found exclusively on the western slopes of the Andes south of Colombia. It occurs sympatrically in some localities (fide *Dodson & Gentry 12815* and *Meerow & Meerow 1140*) with *E. moorei*, though the latter grows at slightly higher elevation in these areas. *Eucharis astrophiala* is the only species of subg. *Eucharis* that enters a definite rest period during the short dry season of the northwestern and central western Ecuadorean Andes. New growth completely ceases, though one or two leaves may persist for the duration.

7. ***Eucharis caucana*** Meerow, sp. nov. TYPE: Colombia. Valle de Cauca: between La Paila and Zarzal, Hacienda El Medio, 975 m, 14 Apr. 1987, *Silverstone-Sopkin et al. 3064* (holotype, FTG; isotypes not seen, CUVC). Figure 87.

Species nova affinis *E. lehmannii* Regel sed floribus breviter pedicellatis grandioribus et paucioribus, stami-

nibus edentatis, et ovulis paucioribus in quoque loculo differt.

Bulb subglobose, 52–60 mm long, ca. 34 mm diam., without an appreciable neck, tunics brown. Leaves 2–3; petiole 21–25 cm long, 7.2–10 mm wide; lamina ovate-elliptic, ca. 25.5 cm long, 10–11 cm wide, plicate, the margins undulate, acuminate, attenuate at the base. Scape 4–5 dm tall, ca. 1 cm diam. proximally, 5 mm diam. distally; bracts 26–27 mm long, 8 mm wide, ovate-lanceolate. Flowers 2–3, slightly declinate, funnelform-campanulate, not fragrant; pedicels ca. 6.5 mm long, ca. 2 mm diam.; tube ca. 32 mm long, 2 mm wide proximally, dilating in its distal $\frac{1}{3}$ to ca. 9.2 mm at the throat, abruptly curved near its base, the dilated portion stained green internally; limb spreading to ca. 3.5 cm, the tepals diverging from the throat at angles of 75–90°; outer tepals ca. 20 mm long, 9.5–10.3 mm wide, ovate, apiculate; inner tepals ca. 18–19 mm long, 11.5 mm wide, ovate, acute to obtuse. Staminal cup ca. 3 mm long (to apex of lobes), edentate, stained green proximally; stamens connate only in the proximal 0.7–1 mm; each filament ca. 10 mm long, narrowly subulate and ca. 1 mm wide in the distal 4–5 mm,

then abruptly dilated proximally to 3 mm wide; anthers oblong, ca. 4 mm long, gray-brown; pollen white, the exine coarsely reticulate, 55–75 μm polar diam., 98–110 μm longest equatorial diam. Style white, ca. 50 mm long, exerted ca. 1 cm beyond the anthers; stigma ca. 2 mm wide, greenish white. Ovary globose-trigonous, 7–7.5 mm diam., ovules 4–6 per locule. Capsule leathery, orange, ca. 1.5 cm long, 2.5 cm wide; seeds 2 per locule, ellipsoid, ca. 10 mm long, ca. 5 mm wide with a smooth, lustrous black testa. Chromosome number: $2n = 138$.

Named for the Río Cauca valley of Colombia to which the species is endemic.

Distribution. Endemic to Valle de Cauca Department in the vicinity of La Paila in western Colombia (Fig. 81). The type location is a 12.5-hectare remnant of primary forest planted with cacao in which canopy trees were retained for shade (*Anacardium excelsum*, *Nectandra caucana*).

Additional specimen examined. COLOMBIA. VALLE DE CAUCA: La Paila, 30 May 1853 (fr), *Holton s.n.* (NY).

The recent receipt of material collected by Phil Silverstone-Sopkin and coworkers is the first collection of the subgenus in the largely deforested Cauca valley since 1922.

Eucharis caucana has the largest pollen grains in the genus and is the only known hexaploid species of *Eucharis*, with a somatic chromosome number of $2n = 138$ (Fig. 88). As with most other South American peripheral isolates from the Amazonian center of distribution for subg. *Eucharis* (*E. astophiala*, *E. corynandra*, *E. lehmannii*, and *E. oxyandra*), *E. caucana* exhibits some degree of morphological novelty; in this case, reduction of staminal connation, funnellform-campanulate perianth, and very large pollen grains. Nonetheless, *E. caucana* has fruit and seed morphology typical of subgenus *Eucharis*. By its reduced staminal cup *E. caucana* shows affinity with *E. lehmannii* from which it differs by having larger flowers, shorter pedicels, straighter tubes, edentate androecia, and fewer ovules per locule. By its high polyploid chromosome number, short pedicels, and flower size, *E. caucana* shows similarity to certain populations of *E. bouchei* var. *bouchei*. Some collections of the latter from Colón Province exhibit funnellform-campanulate perianth morphology and floral tube habit like *E. caucana*. The discovery of this hexaploid species in Colombia supports the hypothesis that a polyploid complex of *Eucharis* may have existed in

Colombia in the recent geologic past (Meerow, 1987d).

8. *Eucharis ulei* Kränzlin, Bot. Jahrb. 50, Beibl. 111: 4–5. 1913. *Urceolina ulei* (Kränzlin) Traub, Pl. Life 27: 57–59. 1971. TYPE: Brazil. Amazonas: Juruá Miry, June 1901, *Ule 5737a* (holotype, B), non *Ule 5737b* (in fruit) (B) vel *Ule 5737* (MG). Figure 89B, C.

Eucharis ipariensis (Ravenna) Ravenna, Phytologia 57: 95. 1984. *Urceolina ipariensis* Ravenna, Pl. Life 38: 50–51. 1982. TYPE: Peru. Huánuco: Pachitea, Honoria, Bosque Nacional de Iparia, Río Pachitea, 20 km above confluence with Río Ucayali, near Miel de Abeja, 1 km from Tuernavista, 26 Apr. 1967, *Schunke 1887* (holotype not seen, NY; isotypes, F, COL, G, US).

Eucharis moana (Ravenna) Ravenna, Phytologia 57: 95. 1984. *Urceolina moana* Ravenna, Pl. Life 38: 50. 1982. TYPE: Brazil. Acre: Río Moa at Serra da Moa village, 27 Apr. 1971, *Prance et al. 12491* (holotype, NY; isotypes, K, MO, not seen: herb. Ravenna).

Eucharis boliviensis Ravenna, Phytologia 64: 218. 1988. TYPE: Bolivia. El Beni: Covendo, 600 m, 19 Aug. 1921, *White 930* (holotype, NY; isotype, K).

Bulb subglobose, (2.5–)3.5–4.5(–5) cm long, 2–3.5(–4.5) cm in diam.; neck 1–2 cm long, ca. 1.5 cm wide; outermost tunics gray-brown, inner tunics tan. Leaves 2–3; petiole (10–)18–30(–35) cm long, 5–6 mm thick; lamina (narrowly) elliptic (average length:width > 3), 18–25(–33) cm long, (5–)7–10(–12.5) cm wide, acute to shortly acuminate, attenuate at the base. Scape (35–)40–58 cm tall, 8–10 mm diam. proximally, 3–4 mm diam. distally; bracts lanceolate to ovate-lanceolate, (25–)30–37(–54) mm long, greenish white. Flowers (3–)7, pendent, without fragrance; pedicels (8–)11–15(–20) mm long, ca. 2 mm diam.; tube (25–)28–35(–37.5) mm long, curved gradually for most of its length, 1.5–2(–2.5) mm wide for most of its length, abruptly dilated just below throat to (6–)7–10 mm; limb spreading to 40–45(–55) mm wide; outer tepals ovate-lanceolate, 24–28(–32) mm long, (6.5–)8–10(–11) mm wide, apiculate; inner tepals ovate, 23–27(–30) mm long, (9–)10–13(–15) mm wide, acute. Staminal cup funnellform-cylindrical, 10–12 mm long (to apex of teeth or lobes), 11–13(–16) mm wide, usually bidentate between each free filament, rarely edentate, irregularly toothed, or the teeth obscure (in which case the stamens quadrately lobed), cleft between each stamen for (1.5–)2–3(–4) mm, with a \pm rectangular, green zone in the proximal half of each stamen; teeth acute or obtuse, 0.5–0.7 mm long; each stamen 3.5–4.5(–5.5) mm wide from tooth to tooth; free filament subulate, (3–)4.5–6 mm long, (1–)1.5–2

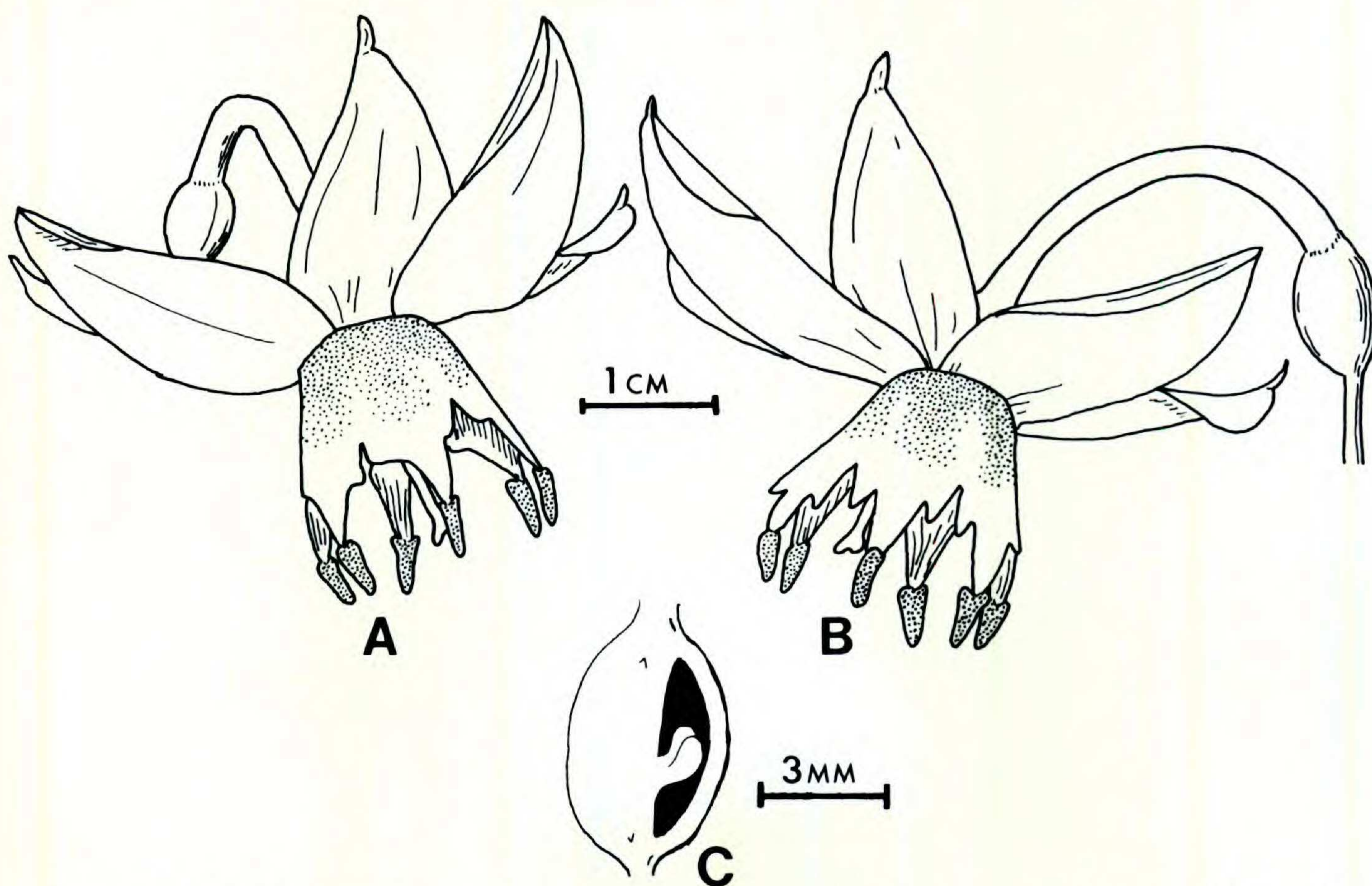


FIGURE 89. *Eucharis cyaneosperma* and *E. ulei*.—A. Flower of *E. cyaneosperma* (holotype, Meerow 1032, FLAS).—B. Flower of *E. ulei* (Schunke 1887, F).—C. Ovary of *E. ulei*, longitudinal section (Schunke 1887, F).

mm wide at its base; anthers oblong, 3–3.8 mm long; pollen grain ca. 49.35 μm polar diam., ca. 69.85 μm longest equatorial diam. Style (40–)45–50(–60) mm long; stigma 1.5–2.5 mm wide. Ovary globose-ellipsoid, 6–8.5(–10) mm long, 4–5.5 mm wide; ovules 2(–4) per locule, superposed in the lower half of the cell. Capsule 1.2–1.5 cm long, 2–2.5 cm wide, bright orange, leathery; pedicels 2–4 cm long; seeds 1–2 per locule, ellipsoid, 8–10 mm long, ca. 5 mm wide with a smooth, lustrous black testa.

Distribution. Understory of primary rain forest in the Amazon Basin and eastern Andean foothills, most common in Peru but sporadically encountered north to Colombia and south to Bolivia (Fig. 81), on fertile, usually noninundated, soils; 100–300(–1,000) m. Flowering at any time of the year, most frequently June–September.

Additional specimens examined. BRAZIL. AMAZONAS: basin of Río Juruá, Foz da Tarauca, Yuma, rare, on varzea land, 1 June 1933, Krukoff 4613 (NY); basin of Río Juruá, near mouth of Río Embira, 7°30'S, 70°15'W, 3 June 1933 (fr), Krukoff 4637 (G, GH, K, NY, S, US); Río Purus, Río Itaxi, Seringal Jurucua, 120 km south of Labrea, 29 June 1971, Prance et al. 13915 (MO, NY). PARA [?]: no data, Ferreira s.n. (P). COLOMBIA: AMAZONAS: Trapecio, confluencia de Río Loretoyacu con el Río Amazonas, Puerto Nariño, Mar. 1968, Diaz-M 15 (COL); Trapecio amazonico, Boiauassu River, 100 m, Oct. 1946,

Schultes & Black 8608a (US); Puerto Nariño, mouth of Río Loretoyacu, 100 m, 8 May 1972 (fr), Plowman 3216 (COL, K). PERU. AMAZONAS: Río Santiago, canto de la Quebrada Caterpiza, 200 m, 11 Sep. 1979 (fr), Huashikat 524 (MO); valle de Río Santiago, ca. 65 km norte de Pinglo, Quebrada Caterpiza, 2–3 km atras de la comunidad de Caterpiza, 200 m, 13 Oct. 1979 (fr), Huashikat 930 (MO); same locality, 17 Dec. 1979, Huashikat 1553 (MO); Monte del Isla, la isla 1 km bajo de La Poza, Río Santiago, 180 m, 8 Aug. 1979 (fr), Leveau 7 (MO); same locality, 15 Aug. 1979 (fr), Leveau 123 (MO); same locality, 8 Aug. 1979 (fr), Pena 9 (MO). LORETO: Río Amazonas, SE of Iquitos, swampy forest, 17 Aug. 1972, Croat 19289 (MO); Río Napo near Entrada de Isla Inayuga, edge of forest, 20 Sep. 1972 (fr), Croat 20521 (MO); near Base Araguana, upper Río Mazán, ca. due north of Santa Maria de Nanay, noninundated forest, 9 July 1976 (fr), Gentry & Revilla 16586 (MO); Maynas, Quebrada Yanomono, Explorama Tourist Camp, halfway between Indiana and mouth of Río Napo, mature noninundated forest on laterite, 4 Nov. 1979 (fr), Gentry et al. 27438 (MO); Yanomono, Explorama Tourist Camp, Río Amazonas above mouth of Río Napo, 72°48'W, 3°28'S, 130 m, upland forest on lateritic soil, 25 June 1982 (fr), Gentry et al. 37204 (MO); Río Samiria, Flor de Yarina, ca. 5°2'S, 74°30'W, 160 m, noninundated restinga forest, Gentry et al. 38103 (MO); Iquitos, ca. 100 m, 3–11 Aug. 1929, Killip & Smith 27442 (US); Yurimaguas, lower Río Huallaga, ca. 135 m, 23 Aug.–7 Sep. 1929, Killip & Smith 27656 (US); Río Maraño Valley, San Lorenzo, between mouths of Río Pastaza and Río Huallaga, 150 m, 20 Aug.–9 Sep. 1929, Killip et al. 29227 (US); Iquitos, Muena-Caño, 105 m, 9 Feb. 1932, Mexia 6504a (F, UC); Maynas, Río Amazonas near Tamishiyacu, 3 Sep. 1976, Revilla 1281 (MO); Pebas on Amazon

River, 25 July 1929 (fr), *Williams 1751* (F); Pebas on Amazon, 21 July 1929 (fr), *Williams 1787* (F); La Victoria on the Amazon, 21 Aug. 1929, *Williams 2629* (F); same locality as preceding, 29 Aug. 1929, *Williams 2938* (F); alto Río Itaya (San Antonio), 145 m, Sep.–Oct. 1929 (fr), *Williams 3398* (F); Puerto Arturo, Yurimaguas, lower Río Huallaga, 155–210 m, 16 Nov. 1929 (fr), *Williams 5148* (F). PASCO: Oxapampa, Palcazu valley, Cabeza de Mono, 5–6 km W of Iscosacin, 17–20 Apr. 1983, *Smith 3787* (MO); SAN MARTÍN: Mariscal Cáceres, Tocache Nuevo, Quebrada de Cachiyacu de Huaguisha, 570 m, 16 July 1982 (fr), *Meerow et al. 1023* (FLAS); Mariscal Cáceres, Tocache Nuevo, Quebrada de Cachiyacu de Huaguisha, 570 m, 16 July 1982, *Meerow et al. 1024* (FLAS); Mariscal Cáceres, Mirama, N of Tocache Nuevo, along left bank of Río Huallaga, 500 m, *Plowman & Kennedy 5811* (GH); Mariscal Cáceres, Tocache Nuevo, Fundo La Campina, 2 km abajo de Tocache Nuevo, margen derecha del Río Huallaga, 400 m, 7 Sep. 1969, *Schunke 3396* (F, US); Mariscal Cáceres, Tocache Nuevo, Quebrada de Cachiyacu, 3 km abajo de Puerto Pizano (margen derecha del Río Huallaga), 21 Apr. 1971. UCAYALI: Coronel Portillo, Yarina Cocha, Fundo “El Pescador,” cerca al Caserío Nuevo Destino, al este de Yarina Cocha, 150 m, 31 Oct. 1984, *Schunke 14153* (FLAS).

Eucharis ulei is among the more widespread Amazonian taxa of subg. *Eucharis*, extending north from its Peruvian center of distribution into Colombia and south to Bolivia (Fig. 81). The species is best recognized by its primarily narrow-elliptic leaves, chiefly five-flowered inflorescence, tube length of ca. 3–4 cm, limb spread of 4–5 cm, and reduced ovule number (generally two per locule, Fig. 89C). Both flower and ovule number have become nearly fixed throughout the range of the species. *Eucharis castelnaeana* is sympatric with *E. ulei* at times but tends to occur on seasonally inundated soils. Flower size and number, ovule number, and chromosome morphology (Meerow, 1987b) suggest close relationship to *E. cyaneosperma*, which has different tube morphology, a deeply trigonous ovary, and blue-coated seeds.

Ravenna (1982: 50) described *Urceolina moana*, citing the “absence of lobes, or teeth, in the cup.” The single, poorly preserved, fragmentary flower of the holotype, however, had stamens at least shortly dentate to quadrate. As in *E. candida* and *E. formosa*, androecial toothiness in *E. ulei* has little taxonomic significance. The androecial morphology of *E. moana* is well included within the range of variation for this character in *E. ulei* (Fig. 70D)—several collections of *E. ulei* have completely edentate staminal cups (e.g., *Meerow et al. 1024*, *Plowman & Kennedy 5811*, *Prance et al. 13915*). Much the same argument applies to the likewise synonymous *E. boliviensis* (Ravenna, 1988), represented by the only specimen of *E. ulei* collected in Bolivia. The only other collection assigned by Ravenna (1988) to *E. boliviensis* (*Cardenas 1553*)

belongs to *E. cyaneosperma*. *Eucharis ipariensis*, inexplicably described by Ravenna (1982) as allied to *E. mastersii* (= *E. × grandiflora* of subg. *Heterocharis*), is also indistinguishable from numerous collections of *E. ulei*.

Kränzlin (1913) and Macbride (1936) noted the dissimilarity of the two specimens comprising the holotype of *E. ulei* (*Ule 5737b*), one in flower, the other in fruit. I have assigned the fruiting specimen (*Ule 5737b*), with blue seeds, to *E. cyaneosperma* Meerow. When a putative isotype of *Ule 5737* was received from MG, it proved to represent *E. castelnaeana*. *Ule* thus collected three species under a single number, an unsurprising occurrence in areas where several *Eucharis* species are sympatric.

9. *Eucharis cyaneosperma* Meerow, Sida 12: 29–49. 1987. TYPE: Peru. San Martín: 20 km N of Tocache Nuevo on road to Tarapoto, Río Cañuto, 520 m, 17 July 1982, *Meerow et al. 1032* (holotype, FLAS). Figure 89A.

Bulb subglobose, 3–5 cm long, 3–3.5 cm diam., tunics light brown. Leaves 2–4; petiole (10–)15–30(–35) cm long, 5–6.5 mm thick; lamina (ovate-)elliptic, 18–25(–30) cm long, (6.5–)7–8(–13) cm wide, apically acute to shortly acuminate, attenuate at the base. Scape (3–)4–5(–6.5) dm tall, 5–7 mm diam. proximally, 3–4 mm diam. distally; bracts ovate-lanceolate, (20–)27–35 mm long. Flowers (3–)5(–7), pendent, without fragrance; pedicels (10–)15–25(–28) mm long, ca. 1.7–2 mm diam.; tube 30–40 mm long, 1.5–2 mm diam. for most of its length, dilating abruptly to 7–9 mm proximal to the throat, curved abruptly ca. 5 mm above the ovary and then \pm straight; outer tepals 23–28(–32) mm long, 8–10(–13) mm wide, ovate-lanceolate, apiculate; inner tepals 21–24(–30) mm long, 10–14(–15) mm wide, ovate, acute to minutely apiculate. Staminal cup cylindrical, (8–)10–12 mm long (to tooth or lobe), 10–13(–15) mm wide, pale yellow or green proximally, quadrate or irregularly toothed between each free filament, the teeth when present < 1.5 mm long, cleft between each stamen 2–3 mm deep; each stamen 3.5–4(–5) mm wide at the base; the narrow, subulate free filament (3–)3.5–4.5(–5.5) mm long, ca. 1.5 mm wide at the base; anthers ca. 3 mm long, oblong; pollen grain ca. 47.95 μ m polar diam., ca. 67.55 μ m longest equatorial diam. Style 4.5–6 cm long, exerted 0.5–1 cm beyond the anthers; stigma 2–2.5 mm wide. Ovary subglobose and deeply trigonous at anthesis, 5–7 mm long, 7–10 mm wide, usually wider than long; ovules

2(-3, 5) per locule, superposed in the lower half of the cell. Capsule 10-12 mm long, 15-20 mm wide, bright orange, leathery; pedicel 25-36 mm long; seed ellipsoid, 7-9 mm long, ca. 5 mm wide, with a lustrous, cobalt blue testa. Chromosome number: $2n = 46$.

Distribution. Sporadic in the understory of premontane to lower montane rain forest of the Amazon basin and eastern Andean foothills, from Peru to Bolivia (Fig. 81), 120-800(-1,200) m elevation. Flowering at any time of the year, most commonly in August.

Additional specimens examined. BOLIVIA. EL BENÍ: vicinity of Rurrenabague, 330 m, 25 Nov. 1921, *Cardenas 1179* (AA, NY, US); Rurrenabague, 500 m, 7 Oct. 1921, *Cardenas 1553A* (NY); San Antonio, 15 Nov. 1958, flowered in cultivation 30 Apr. 1959, *Nelson 58-301* (MO); same collection as preceding, flowered in cultivation 4 Apr. 1961, *Nelson 58-301* (MO). BRAZIL. ACRE: basin of Río Purus, near mouth of Río Macauhan, 9°20'S, 69°W, 17 Aug. 1933, *Krukoff 5573* (NY); Río Branco de Obidos, Santo Antonio, 6 Aug. 1912, *Ducke 12162* (GOET, photo and fragment F). AMAZONAS: Juruá Miry, June 1901, *Ule 5737b* (B). PERU. CUZCO: Río Araza, northeast of Cuzco, 1,150 m, Jan. 1943, *Sandeman 3724* (K, OXF). LORETO: Maynas, arriba del Puerto Belen, Río Itaya, 73°25'W, 3°58'S, 120 m, 16 Nov. 1978 (fr), *Diaz et al. 621* (MO); Maynas, Yanamono, Explorama Lodge, 72°45'W, 3°25'S, 120 m, 29 May 1979 (fr), *Diaz et al. 1125* (MO); Reguena, Cocha Iricahua, Río Ucayali, 31 May 1982, *Encarnación 26186* (MO); Maynas, Yanamono, Explorama Tourist Camp, Río Amazonas halfway between Indiana and mouth of Río Napo, 72°50'W, 3°28'S, 120 m, 28 Aug. 1983, *Gentry et al. 43758* (MO); Flor de Yarina (Río Samiria), 22 Aug. 1983 (fr), *Vasquez et al. 4297* (MO); Ucayali, Canchahuayo (Isla Banos), 75°10'W, 7°5'S, 200 m, 29 Nov. 1985 (fr), *Vasquez et al. 6997* (MO); lower Río Nanay, 24 May 1929 (fr), *Williams 431* (F); La Victoria on Amazon, 21 Aug. 1929 (fr), *Williams 2619* (F); La Victoria on Amazon, 28 Aug. 1929 (fr), *Williams 2878* (F, US). JUNÍN: Puerto Yessup, ca. 400 m, 10-12 July 1929 (fr), *Killip & Smith 26394* (F, NY, US); Río Negro to Satip, 800 m, 17 Aug. 1960, *Woytkowski 5830* (MO). MADRE DE DIOS: Tahuamanu, Iberia, 200 m, 15 Nov. 1973 (fr), *Alfaro 1684* (MO); Iberia, Miraflores, vicinity Río Tahuamanu, 1 Sep. 1945, *Seibert 2145* (US). SAN MARTÍN: (fr), *Schunke 4843* (F, US); Mariscal Cáceres, Tocache Nuevo, Quebrada de Huaguisha (margen derecha del Río Huallaga, 400-450 m, 3 July 1974 (fr), *Schunke 7146* (F). UCAYALI: middle Ucayali, Cashiboplaya, 10°S, 1923, *Tessman 3179* (G, NY, S).

Eucharis cyaneosperma is the only species of *Eucharis* with blue-coated seeds. The species appears very similar to *E. ulei* but differs by having usually shorter leaves, different tube morphology (abruptly curved at the base in *E. cyaneosperma*, sinuously curved in *E. ulei*), irregularly dentate to quadrate staminal cup (Fig. 89A), deeply trigonous ovary, and different seed color. In the southern

part of its range, *E. cyaneosperma* occupies more upland sites than are usually characteristic of *E. ulei*.

10. *Eucharis lehmannii* Regel, Gartenfl. 38: 313-314, t. 1300, fig. 1. 1888. *Urceolina lehmannii* (Regel) Traub, Pl. Life 27: 57-59. 1971. TYPE: Colombia. Cauca: ex hort. Regel, from bulbs collected by Lehmann near Popayan, Apr. 1888, *Regel s.n.* (holotype (fragmentary), LE; photo of holotype, FLAS, K). Figure 90D-F.

Bulb subglobose, not seen. Leaves 2; petiole 45.5 cm long, 3.5 mm thick; lamina ovate-elliptic, 24-25 cm long, 16 cm wide, short acuminate, basally subcordate and attenuate to the petiole. Scape not seen; bracts lanceolate; bracteoles linear-lanceolate. Flowers 4; pedicels to 30 mm long; limb patent, spreading to ca. 4 cm; tube ca. 25 mm long, ca. 1.2 mm wide below, dilating abruptly to 8 mm at the throat; outer tepals 20-22 mm long, 8-10 mm wide, ovate-lanceolate, acute-apiculate; inner tepals 18-20 mm long, 10-12 mm wide, obtuse. Staminal cup 7-8 mm long (to apex of tooth), deeply cleft between each stamen to < 2 mm from the throat; each stamen bidentate, the teeth long-lanceolate, as long as the free filament; free filament linear, 7-8 mm long, ca. 1 mm wide; anthers sub-basifixed, versatile. Style slightly exerted beyond the anthers. Ovary globose-ellipsoid, ca. 6 mm long, ca. 4 mm wide; ovules ca. 10 per locule. Fruit and seed unknown.

Distribution. Extremely rare in the understory of moist, lower montane forest of the Cordillera Oriental in Cauca Department of Colombia (Fig. 91), 1,200 m.

Additional specimen examined. COLOMBIA. CAUCA: Aganche, Río Orejas, 1,200 m, *Lehmann 5883* (K).

Eucharis lehmannii is known only from the fragmentary type (a single flower) and a single specimen at Kew with only one flower present. An Ecuadorean specimen mislabeled as the type of *E. lehmannii*, received from Kew (*Lehmann 7775*), turned out to be *E. astrophiala* (Ravenna) Ravenna. Like *E. caucana*, to which it may be very closely related, *E. lehmannii* is a peripheral isolate of subg. *Eucharis*, with novel androecial character states. Despite the unusual staminal morphology, the plant figured in Regel's (1889) description resembles *Eucharis* subg. *Eucharis* by overall morphology and habit of the flower. In 1984, I was not able to collect this species successfully at the

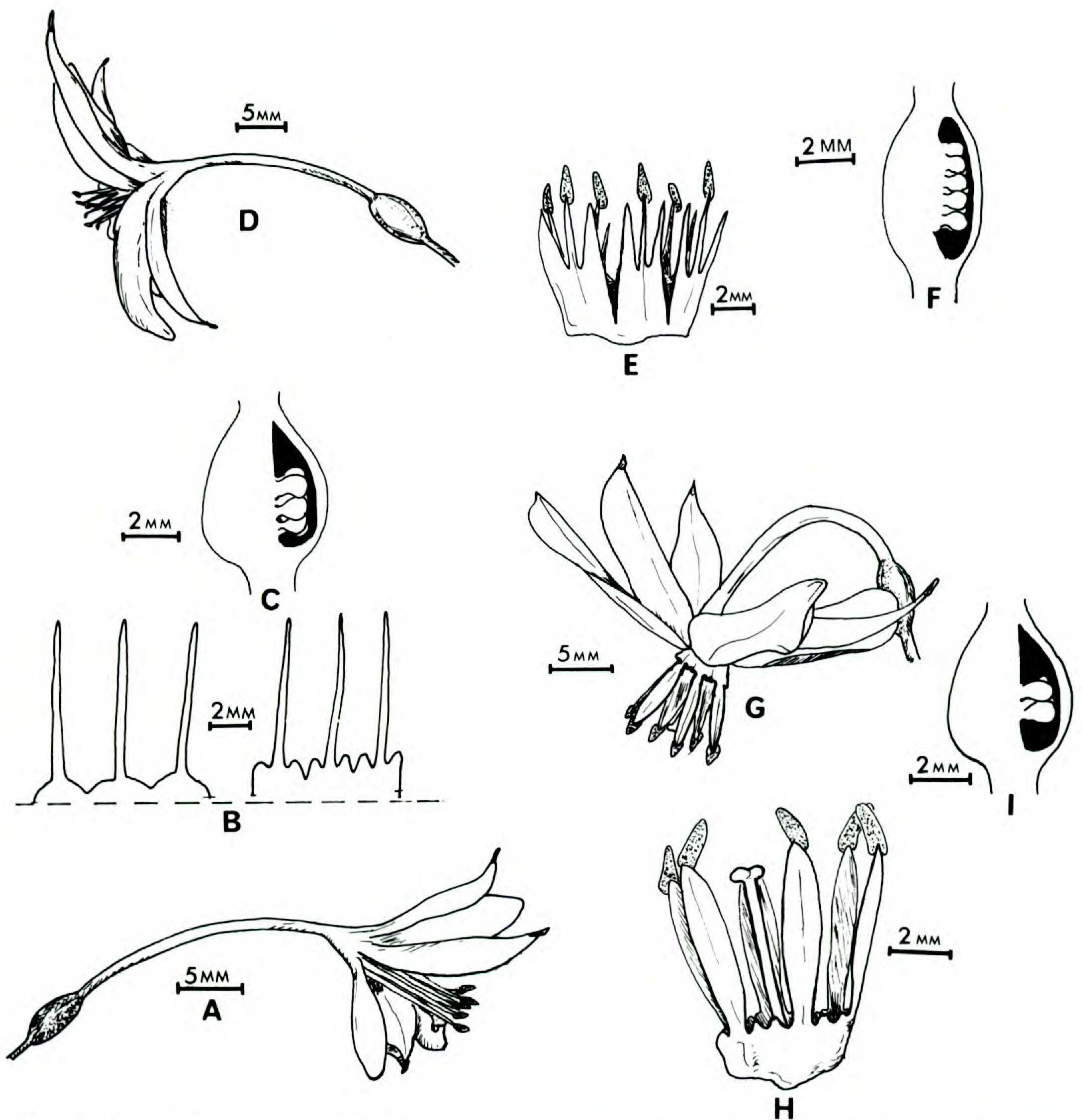


FIGURE 90. *Eucharis corynandra*, *E. lehmannii*, and *E. oxyandra*. A-C. *E. oxyandra* (isotype: Hutchison et al. 5983, UC).—A. Flower.—B. Androecium. Note the polymorphism.—C. Ovary, longitudinal section. D-F. *E. lehmannii* (after tab. 1300 in Regel, 1889, and a photo of the type at LE).—D. Flower.—E. Staminal cup.—F. Ovary, longitudinal section. G-I. *E. corynandra* (isotype, Ravenna 2090, K).—G. Flower.—H. Staminal cup.—I. Ovary, longitudinal section.

locality of Lehmann 5883 in Colombia, an area now largely deforested.

11. *Eucharis corynandra* (Ravenna) Ravenna, *Phytologia* 57: 95–96. 1985. *Urceolina corynandra* Ravenna, *Pl. Life* 34: 80–81. 1978. TYPE: Peru. Cajamarca: Chinganza, between Aramango and Montenegro, 2 July 1973, Ravenna 2090 (holotype, herb, Ravenna, not seen; isotypes, K, not seen: NY, MO). Figure 90G–I.

Bulb globose, 47 mm long, 37 mm diam.; tunics light brown. Leaves elliptic-lanceolate; petiole 25–

27 cm long, 3.5–5 mm thick; lamina 20–27 cm long, 5 cm wide, apically acute. Scape 50 cm tall, slender, ca. 2 mm diam. distally; bracts lanceolate, ca. 32 mm long. Flowers 8–10; pedicels 15–23 mm long, thin; perianth tube curved, 17–18 mm long, ca. 1 mm wide for most of its length, abruptly dilated to 3–4 mm at the throat; limb spreading to 3–4 cm wide; outer tepals 27–29 mm long, 6–7 mm wide, ovate-lanceolate, acute-apiculate at the apex; inner tepals ca. 28 mm long, 8–10 mm wide; ovate, acute. Staminal cup short, funnellform, thick and waxy in texture, 3.5 mm long, 7.5 mm wide, with two obtuse teeth between each free filament, somewhat plicate; free filaments club-

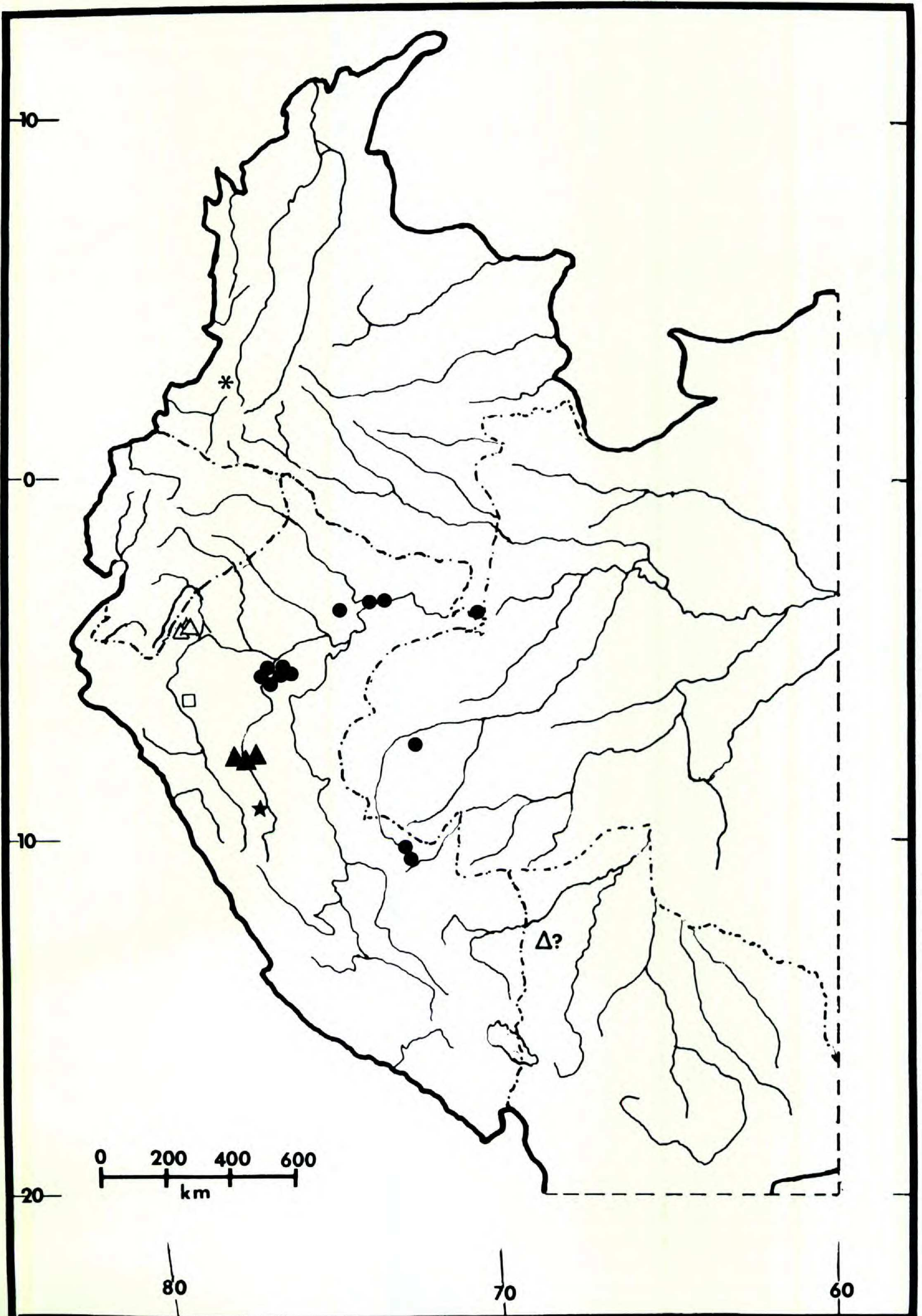


FIGURE 91. Distributions of *Eucharis castelnaeana* (circles), *E. corynandra* (squares), *E. lehmannii* (snowflake), *E. oxyandra* (stars), *E. plicata* subsp. *plicata* (closed triangles), and *E. plicata* subsp. *brevidentata* (open triangles) in northwestern-central South America.

shaped, appearing narrowly elliptic-lanceolate when dry, ca. 6.2 mm long, 1.8 mm wide, abruptly dilated to ca. 1 mm at the base, inserted adaxially between 2 of the teeth; anthers oblong-linear, ca. 3 mm long, versatile, black. Style 30–44.5 mm long, stigma trilobed. Ovary globose-ellipsoid, 6 mm long, 3 mm wide; ovules 4–6 per locule, superposed. Fruit and seed unknown.

Distribution. Known only from the type locality (Fig. 91), in tropical forest on slopes, near a small ravine with *Dieffenbachia* sp., *Heliconia* sp., *Clusia* sp., and *Xyphidium coeruleum* Aubl. Elevation not reported.

In size and number of the flowers, as well as ovule number, *Eucharis corynandra* shows affinity to *E. castelnaeana* (Baillon) Macbr. and to *E. plicata* Meerow. The short staminal cup and distinctive club-shaped free filaments (Fig. 90H) are the principal unique characters of this species. I cannot, however, confirm Ravenna's (1978) description of the anthers as densely pubescent. The collection locality suggests that it is an upland isolate from the Amazonian center of the subgenus, the plant having colonized the lower limits of the "ceja de la selva" forest formations in Cajamarca Department of Peru.

12. *Eucharis oxyandra* (Ravenna) Ravenna [subg. *Eucharis insertae sedis*], *Phytologia* 57: 95–96. 1985. *Urceolina oxyandra* Ravenna, *Wrightia* 7: 251–253. 1983. TYPE: Peru. Huánuco: Huánuco, Río Chinchao, below Carpish on rd. to Tingo Maria, 1,800 m, 19 July 1964, *Hutchison et al.* 5983 (specimens prepared from bulbs flowered in cultivation at UC, 26 Apr. 1967) (holotype, USM, not seen; isotypes, MO, UC). Figure 90A–C.

Bulb not seen. Leaves (one seen) elliptic; petiole 17 cm long, 4–6 mm thick; lamina 25 cm long, 12 cm wide. Scape 27–28 cm tall; bracts 34–35 mm long, ovate-lanceolate. Flowers 6–7, (crateriform?), cernuous; pedicels ca. 19 mm long; tube curved, 25 mm long, 1.5 mm diam. below, dilated abruptly at the throat to 3.5 mm; tepals spreading to 27 mm wide; outer series 17–19 mm long, 6.7 mm wide, ovate-lanceolate, acute-apiculate; inner series 17–18 mm long, 8–9 mm wide, ovate, obtuse. Staminal cup very short, 0.8–1.5 mm long, 3–3.5 mm wide, edentate or with 2 obtuse teeth between the free filaments; free filaments ca. 7 mm long, ca. 1 mm wide at the base, narrowly subulate; anthers oblong, 3.3 mm long, sub-basifixed, eventually versatile; pollen grain ca. 42.36

μm polar diam., ca. 68.36 μm longest equatorial diam. Style 32.8 mm long; stigma 2–2.5 mm wide. Ovary globose-ellipsoid, 6 mm long, 4 mm wide; ovules 6–8 per locule. Fruit and seed unknown.

Distribution. *Eucharis oxyandra* is not known in the wild state. The collector's field notes (UC) indicate that three bulbs were found at the type locality (Fig. 91) "exposed on surface of ground with evidence of past cultivation, in deep shade near abandoned hut above road. The third bulb proved to be *Urceolina urceolata* (R. & P.) M. L. Green."

This unusual species has the smallest staminal cup of any Peruvian species of *Eucharis* subg. *Eucharis* (Fig. 90B). The long, almost linear, free filaments are another unusual feature of the androecium. The polymorphism of the staminal cup (both edentate and obtusely dentate forms represented in the isotypes, Fig. 90B) is puzzling and adds further credence to my suggestion that this character has been over-weighted as an indicator of species delimitation in the alpha-taxonomic literature relating to the genus. Alternatively, it is possible that the two bulbs found by the collector and representing this species were of two different origins.

In publishing *Urceolina oxyandra*, Ravenna (1983) was apparently unaware of the unusual situation in which the species was found, having examined only a duplicate at USM, which seems to have lacked the detailed field notes of the collector. He argued that the unusual morphology of the androecium (reduced staminal cup and long, narrowly subulate filaments), similar to that of *Urceolina*, supported the inclusion of *Eucharis* within *Urceolina* (Traub, 1971), a position he recently reversed (Ravenna, 1985). This type of androecial morphology is characteristic of two putative intergeneric hybrids between *Eucharis* and *Urceolina*, \times *Urceocharis edentata* Wright (1910) and \times *U. clibranii* Masters (1892).

Given that the plant was discovered as an artifact of cultivation in company with a bulb of *Urceolina*, and in a geographic area of loose sympatry for the two genera, I thought it possible that *E. oxyandra* might represent a hybrid between *Eucharis* and *Urceolina*. \times *Urceocharis edentata* was supposedly collected in the wild in Peru (Wright, 1910). Pollen of *E. oxyandra*, however, stains 100% with Alexander's (1969) stain. Both \times *U. edentata* and \times *U. clibranii* produced very little pollen (Wright, 1910), an observation confirmed when I examined specimens of both hybrids (ex hort. BM). Pollen grain size of the species is more like that of *Eu-*

charis subg. *Eucharis*, but exine sculpturing resembles that of *Urceolina* (Meerow & Dehgan, 1988). Fertile hybrids between closely related genera are not unknown in Amaryllidaceae (Traub, 1963).

Alternatively, *Eucharis oxyandra* might be a relict taxon close to the ancestor of *Urceolina*, a genus whose divergence from *Eucharis* may have been relatively recent (see previous section). Phylogenetic analysis supports this latter hypothesis. At present, it seems best to treat *E. oxyandra* as a species of *Eucharis*, even though its *known* shared characteristics with *Eucharis* are plesiomorphic, since its phylogenetic relationships are obscured by the large amount of unknown character state data. As in *E. astrophiala*, *E. caucana*, *E. corynandra*, and *E. lehmannii*, this species exhibits a pattern of morphological novelty characteristic of peripheral isolation in *Eucharis*.

13. *Eucharis plicata* Meerow, *Brittonia* 36: 18–25. 1984. TYPE: Peru. San Martín: Mariscal Cáceres, Tocache Nuevo, Quebrada de Huaguisha, right bank Río Huallaga opposite Tocache Nuevo, 8°09'S, 76°27'W, 500–600 m, 14 Dec. 1981, *Plowman et al.* 11394 (holotype, FLAS; isotypes not seen, F, K, NY, USM).

Bulb subglobose, 5–6 cm long, 4 cm wide, tunics brown. Leaves 2–4 at anthesis, petiole 25–35 cm long; lamina widely elliptic to ovate, (19–)20–30 (–35) cm long, 7–12(–14) cm wide, short acuminate, very shortly attenuate to the petiole, thin, lustrous dark green adaxially, silvery-green abaxially, abaxial cuticle densely striate. Scape 40–60 cm tall; bracts 29–30 mm long, ovate-lanceolate; bracteoles successively shorter and narrower. Flowers (7–)9–10, sometimes lightly fragrant; pedicel suberect, 10–15(–25) mm long; perianth tube 25–28 mm long, 2.5–3 mm wide throughout most of its length, dilating abruptly to 6–10 mm at the throat; limb spreading to 30–40 mm; tepals ovate, recurved at the apex, subequal; outer series ca. 19–24 mm long, 9–14 mm wide, apiculate; inner series 16–23 mm long, 11–15.5 mm wide, apically acute. Staminal cup campanulate, ca. 8.5–12 mm long (to apex of teeth), 10–12(–15) mm wide, apically white, basally pale greenish yellow, plicately folded on either side of the filamental trace, bidentate; each stamen 4.5–5.5 mm wide, the anther-bearing part subulate, 2–3.5 mm long, apically obtuse; anthers oblong-linear, sub-basifixed, erect at first, then becoming versatile, grayish brown, 3.5–4 mm long; pollen grains 41.3–43.5

μm polar diam., 59.9–68.9 μm longest equatorial diam. Style 36–40 mm long; stigma ca. 2.5 mm wide. Ovary globose-ellipsoid, green, ca. 5–6 mm long, 3.4–4 mm wide; ovules 4–8 per locule. Capsule ca. 1 cm long, 2 cm wide, bright orange, leathery; seeds 1–2 per locule, ca. 1 cm long, 5 mm wide; testa shiny black. Chromosome number: $2n = 46$.

KEY TO THE SUBSPECIES OF *EUCCHARIS PPLICATA*

- 1a. Flowers not noticeably fragrant; perianth tube dilating to 6–7.5 mm at the throat; staminal cup deeply plicate, ca. 12 mm long to apex of teeth; teeth longer than subulate portion of filament, coarsely serrulate, imbricate; style reaching to half the length of the cup; ovules 7–8 per locule 12a. *E. plicata* subsp. *plicata*
1b. Flowers mildly fragrant; perianth tube dilating to 7.5–10 mm at the throat; staminal cup only shallowly plicate, ca. 8–10 mm long to apex of teeth; teeth shorter than subulate portion of filament, entire, nonimbricate; style reaching to just below the teeth; ovules 4–5(–7) per locule 12b. *E. plicata* subsp. *brevidentata*

12a. *E. plicata* subsp. *plicata*. Figure 92.

Flowers without noticeable fragrance; pedicel suberect, 10–15 mm long; perianth tube 22–24 mm long, dilating abruptly to 6–7.5 mm wide at the throat; outer tepals 18–23 mm long, 9–12 mm wide; inner tepals 16–20 mm long, 11–12 mm wide. Staminal cup ca. 12 mm long and wide, deeply plicate on either side of the filamental trace; the anther-bearing portion of each filament inserted between 2 irregular, obtuse, coarsely serrulate teeth, each 4–5 mm long, adjacent pairs somewhat imbricate and appearing as one; pollen grain ca. 43.45 μm polar diam., ca. 68.9 μm longest equatorial diam. Style reaching to ½ the length of the staminal cup. Ovules 7–8 per locule.

Distribution. Known only from the type locality, where it is locally abundant (Fig. 91). This population appears to have hybridized with *E. ulei* and contains a range of intermediate morphs in addition to true *E. plicata*. The intermediates show reduced pollen stainability, the presence of non-homologous chromosomes, and extreme allozyme heterogeneity. It is unclear whether these represent a highly variable F_1 , the F_2 , or the results of introgression with *E. plicata* subsp. *plicata*. An analysis of this population is in preparation.

Additional specimens examined. PERU. SAN MARTÍN: same locality as the type, 16 July 1982, *Meerow et al.* 1025 (FLAS); same locality as the type, 4 Aug. 1974, *Schunke* 8046 (F). *Putative hybrids with E. ulei:* PERU.

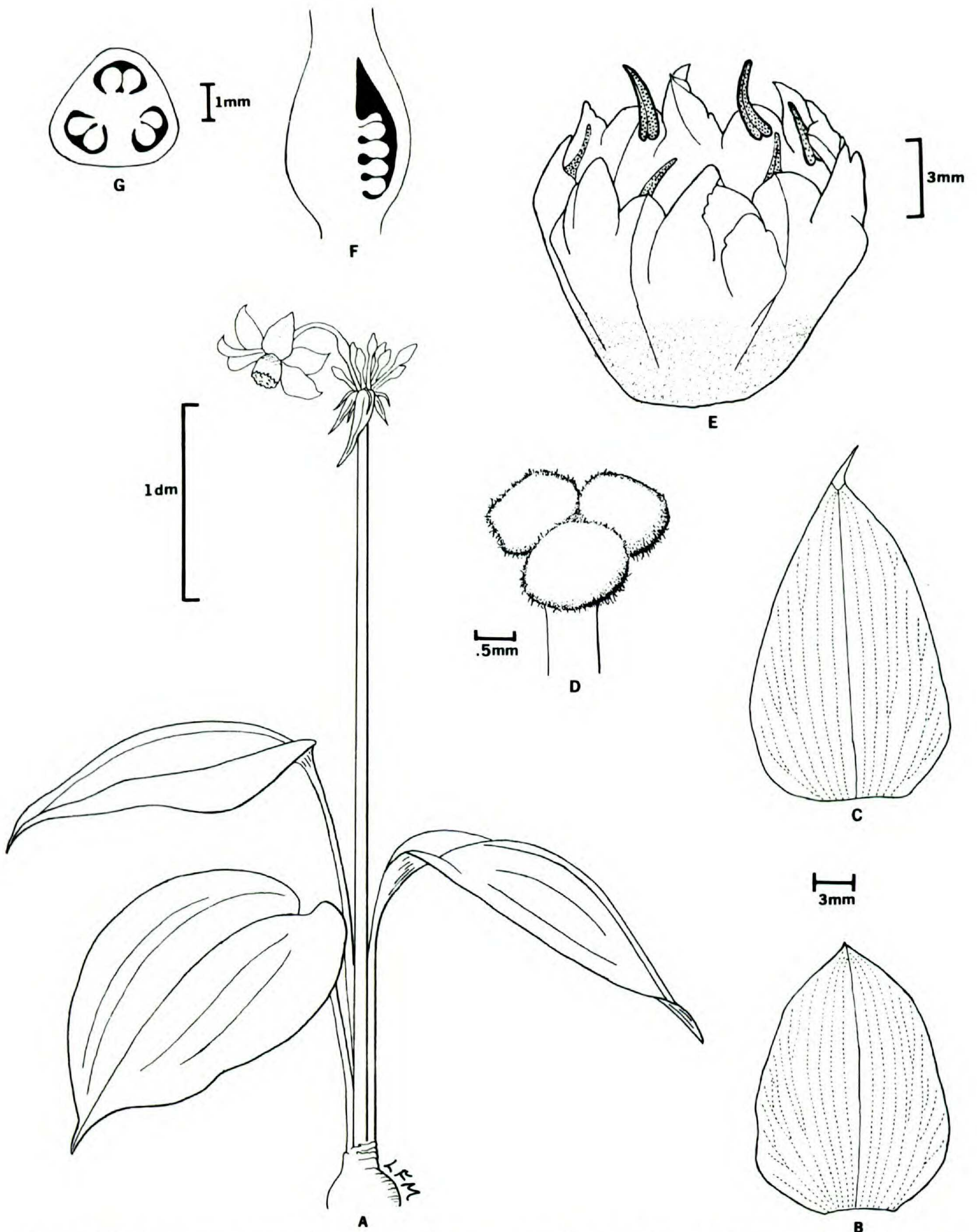


FIGURE 92. *Eucharis plicata* subsp. *plicata* (Meerow et al. 1025, FLAS).—A. Habit.—B. Inner tepal.—C. Outer tepal.—D. Stigma.—E. Staminal cup.—F. Ovary, longitudinal section.—G. Ovary, transverse section.

SAN MARTÍN: same locality as the type, 16 July 1982, Meerow et al. 1030, 1031 (FLAS).

13b. *E. plicata* subsp. *brevidentata* Meerow, subsp. nov. TYPE: Bolivia. El Beni [?]: no collection information, ex hort. Fairchild Trop-

ical Garden from collections by Fred Fuchs, Jr., 3 Oct. 1984, Meerow 1143 (holotype, FLAS).

Subspecies nova differt a subspecies typica dentibus staminalibus brevioribus et non serrulatis vel imbricatis.

Flowers mildly fragrant; perianth tube 25–29 mm long, dilating abruptly to 7.5–10 mm wide at the throat; outer tepals 20–24 mm long, 9–12 mm wide; inner tepals 18.7–23 mm long, 12–15 mm wide. Staminal cup 8–11 mm long (to apex of teeth), 10.5–14 mm wide, only shallowly plicate; teeth ca. 1.5–2 mm long, reaching to about half the length of the subulate portion of the filament, obtuse, entire, nonimbricate; pollen grain ca. 41.3 μm polar diam., ca. 59.9 μm longest equatorial diam. Style reaching to just below the apex of the teeth. Ovules 4–6(–8) per locule.

The epithet of this subspecies refers to the short teeth of the staminal cup.

Distribution. Rare in the understory of premontane and lower montane rain forest of north-central Peru and Bolivia (Fig. 91), 200–420 m. Flowering August–October.

Additional specimens examined. PERU. AMAZONAS: Río Cenepa, vicinity of Huampami, ca. 5 km E of Chavez Valdivia, ca. 78°30'W, 4°30'S, 200–250 m, 11 July 1978 (fr), *Ancuash 1024* (MO); Río Cenepa, 10–12 km NW of Huampami, ca. 420 m, 2 Oct. 1972, *Berlin 148* (NY); Río Cenepa, vicinity of Huampami, ca. 5 km E of Chavez Valdivia, Quebrada Huampami, ca. 78°30'W, 4°30'S, 200–250 m, 15 Aug. 1978, *Kujikat 365* (MO).

Eucharis plicata is phenetically and cladistically closest to *E. castelnaeana*. The phenetic relationship between the two species is most evident in *E. plicata* subsp. *brevidentata*, which in characteristics of the staminal cup and ovule number is intermediate between subsp. *plicata* and *E. castelnaeana*. From the latter, *E. plicata* may be distinguished by its wider leaves and tepals, larger flowers, campanulate staminal cup which is plicate along the filamental traces (Fig. 92E), more numerous ovules, and fruit and seed morphology typical of subg. *Eucharis*.

14. *Eucharis castelnaeana* (Baillon) Macbride, Publ. Field Mus. Nat. Hist. Bot. Ser. 11: 47. 1931. *Caliphruria castelnaeana* Baillon, Bull. Mens. Soc. Linn. Paris 144: 1133–1136. 1894. *Urceolina castelnaeana* (Baillon) Traub, Pl. Life 27: 57–59. 1971. TYPE: Peru. Ucayali: Pampa del Sacramento, June 1847, *Castelnau s.n.* (holotype, not located; isotype, P). Figure 93.

Eucharis narcissiflora Huber, Bol. Mus. Goeldi Para 4: 543. 1906. *Urceolina narcissiflora* (Huber) Traub, Pl. Life 27: 57–59. 1971. TYPE: Peru. Ucayali: Sarayacu, Catalina, 25 June 1898, *Huber 1574* (holotype, MG; isotype (photo and fragment), F).

Bulb small, subglobose, 2.2–3(–4.5) cm long,

1.4–2.7 cm wide; neck 1–2 cm long, 1–1.5 cm wide; tunics tannish brown. Leaves 2–4; petiole (10–)13–17(–25) cm long, 3–6 cm wide; lamina narrowly ovate-elliptic, (10–)15–20 cm long, 5–7(–10) cm wide, apex shortly acuminate, lustrous dark green adaxially, lighter green abaxially, margins undulate. Scape (2.5–)3–4(–5) dm tall, 5–6 mm diam. proximally, ca. 3 mm diam. distally; bracts (2.5–)3–4 cm long, ovate-lanceolate, greenish white. Flowers (7–)8–10, pendent, small, with a faint lemon fragrance; pedicels 10–18 mm long; tube 15–25(–30) mm long, 1–1.5(–2) mm wide for most of its length, abruptly dilated near the throat to 5–6(–8) mm wide; tepals patent, spreading to (2.5–)3–4 cm, often distally recurved, sometimes strongly reflexed for their entire length; outer tepals (ovate-)lanceolate, 15–20 mm long, 5–7 mm wide, apiculate; inner tepals ovate, 11.5–18.7 mm long, 8–11 mm wide, acute. Staminal cup funnelform-cylindrical to cylindrical, usually subcylindrical proximally and abruptly dilated at $\frac{1}{2}$ – $\frac{2}{3}$ of its length, (5.5–)7–8(–9.5) mm long (to apex of tooth), (7–)9–11(–12) mm wide, zoned greenish yellow in the proximal $\frac{1}{3}$ – $\frac{2}{3}$, slightly incurved at the rim, waxy and slightly succulent in texture, bidentate between each free filament, conspicuously plicate between the teeth, very shallowly cleft between each tooth (< 1 mm) and as deep or more deeply cleft between the teeth and the free filament (> 1 mm); teeth 0.5–1 mm long, reaching to about half the length of the free filaments, obtuse, entire; free filament subulate, (1.5–)2–3(–4) mm long, ca. 1.5 mm wide at the base, obtuse or acute; anthers 3–4.5 mm long, oblong, grayish brown, sub-basifixed; pollen grain ca. 39.45 μm polar diam., ca. 55.8 μm longest equatorial diam. Style 25–35 mm long, reaching the apex of the cup or slightly inserted; stigma ca. 1.5 mm wide. Ovary globose, 3.5–5 mm diam., white to greenish white; ovules (2–)4–5(–7) per locule. Capsule subglobose, shallowly trilobed, ca. 1 cm long, 1.5 cm wide, glaucous green, thin-walled, sometimes abscising indehiscently; seeds 1–3 per locule, compressed-ellipsoid, ca. 1 cm long, 5 mm wide; testa dull black, rugose. Chromosome number: $2n = 46$.

Distribution. Understory of lowland and premontane, often seasonally inundated, primary rain forest in the Amazon basin, most commonly in Peru, rare in Colombia and Brazil (Fig. 91), 100–200 m. Flowering June–September (–December).

Vernacular names. Amangay, sachá cebolla.

Additional specimens examined. BRAZIL. AMAZONAS: Río Juruá, Río Miry, July 1901, *Ule 5737* in part (MG). COLOMBIA. AMAZONAS: vicinity Leticia, ex hort. Fairchild

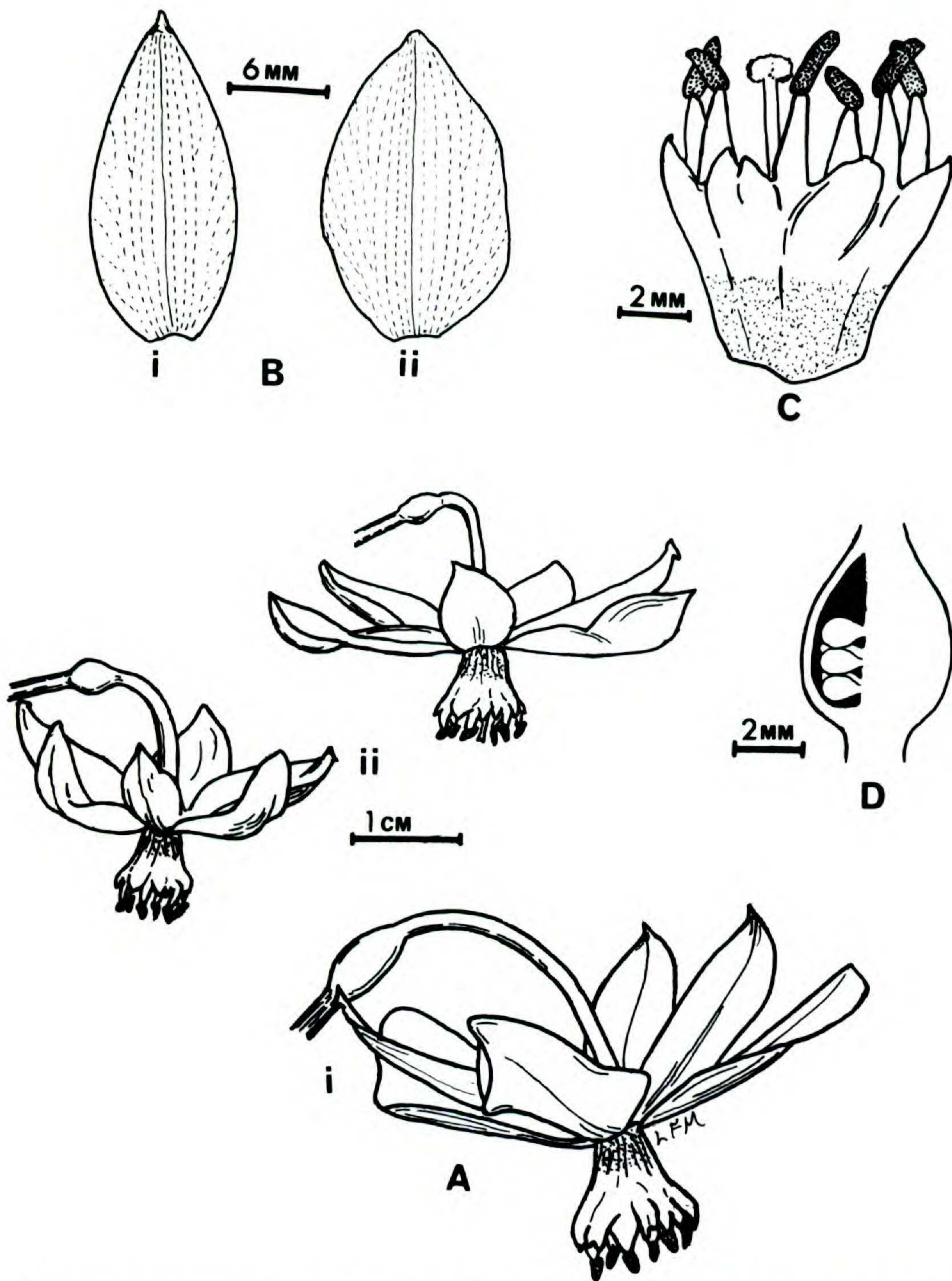


FIGURE 93. *Eucharis castelnaeana*. —A. Flowers. i, *Schunke 14154-A* (FLAS); ii, *Schunke 14156*. Note varying habit of limb. —B. Tepals (*Schunke 14156*). i, outer tepal; ii, inner tepal. —C. Staminal cup (*Schunke 14156*). —D. Ovary (*Schunke 14156*), longitudinal section.

Tropical Garden from collections made by R. Buttons, 1 Apr. 1984, *Watson 1868* (FLAS). PERU. LORETO: Isla Santa María, near Yurimaguas, Huallaga Valley, 150–200 m, 16 Sep. 1948, *Ferreyra 4984* (MO); Maynas, Quebrada Sucusari, Llachapa camp of Explorama, north side of Río Napo below Mazan, forest on somewhat sandy lateritic soil, 140 m, 6 Nov. 1979, *Gentry et al. 27569* (MO); Maynas, Yanamono, Explorama Tourist camp on Río Amazonas between Indiana and mouth of Río Napo, 72°48'W, 3°28'S, seasonally inundated tahuampa, 120 m, 28 July 1980, *Gentry et al. 29203* (MO); Puerto Arturo, lower Río Huallaga below Yurimaguas, ca. 135 m, 24–25 Aug. 1929, *Killip & Smith 27801* (NY, US); same locality, Aug. 1929, *Killip & Smith 27844* (F, NY, US); between Yurimaguas and Balsapuerto (lower Río Huallaga basin), 135–150 m, 26–31 Aug. 1929, *Killip & Smith 28249* (US); Santa Rosa, lower Río

Huallaga below Yurimaguas, ca. 135 m, *Killip & Smith 28886* (F, NY, US); Maynas, Santa María de Nanay, Colonia San Francisco de Indies Yaguas, 1.5 km del Fundo Balcón Momon, 106–110 m, 15 Nov. 1984, *Schunke 14154a* (FLAS); Alto Amazonas, Yurimaguas, camino a “Schunguyce” al sur este de Puerto Arturo, near Yurimaguas, 150–200 m, 1 Dec. 1984, *Schunke 14156* (BM, COL, F, FLAS, G, GB, GH, K, MO, NY, P, S, UC, US); Pebas on the Amazon, 30 July 1929, *Williams 1898* (F, S, US); lower Río Huallaga, Sapotoyacu, Santa Rosa, 155–210 m, 11 Nov. 1929 (fr), *Williams 4906* (F); Puerto Arturo, Yurimaguas, lower Río Huallaga, 155–210 m, 15 Nov. 1929, *Williams 5051* (F).

Eucharis castelnaeana has been collected most frequently in the vicinity of Yurimaguas in Peru

(Fig. 91) and is sometimes locally abundant in rain forest understory. It has the smallest flowers of any species in subg. *Eucharis* and is the major exception to the correlation of reduced flower size with loss of fragrance that otherwise characterizes *Eucharis*. Several living collections produce a mild lemon scent when ambient temperatures are high (as does *E. plicata* var. *brevidentata*). It is the only species of subg. *Eucharis* in which the ripe capsule is not leathery and orange. The glaucous, green, thin-walled capsule is tardily dehiscent and can abscise without opening, though the seeds within are fully ripe.

Eucharis castelnaeana is autogamous. Under greenhouse cultivation it is the only species of *Eucharis* that successfully sets fruit with self-pollen. Unmanipulated inflorescences regularly set 50–75% of their capsules.

Eucharis castelnaeana is variable in leaf and flower size (Fig. 93A) and, to a lesser extent, in androecial morphology. In his description of *E. narcissiflora*, Huber (1906) made reference to *E. castelnaeana*, described from the same location as Huber's type of *E. narcissiflora*, but differentiated his new species solely on the basis of size. The two taxa represent the extremes of size diversity of a single species and differ by no other characters. Populations represented by *Schunke 14154a* (Fig. 93Ai) have flowers almost twice as large as those of *Schunke 14156* (Fig. 93Aii) but are otherwise indistinguishable. Shape of the staminal cup in the latter collection can range from nearly cylindrical to funnellform-cylindrical.

Eucharis plicata is phenetically the closest species to *E. castelnaeana*. Baillon (1894) considered *E. castelnaeana* intermediate between *Caliphruria* and *Eucharis* in his argument for combining these two genera. Baillon probably weighed flower size heavily in his judgment, one of only two characters by which *E. castelnaeana* resembles *Caliphruria*. In Baillon's time, most other small-flowered *Eucharis* species were not yet described. Additionally, the green, thin-walled capsule of *E. castelnaeana* is like the fruit of *Caliphruria*. Baillon (1894) gave no indication whether he was familiar with the fruit of either *Eucharis* or *Caliphruria*. Nonetheless, perianth and pollen exine morphology place *E. castelnaeana* squarely in *Eucharis* despite its aberrant fruit and seed morphology.

***Eucharis* subg. *Heterocharis* Meerow, subg. nov.**

TYPE SPECIES: *Eucharis* × *grandiflora* Planchon & Linden, Fl. Serres Jard. Eur. Ser. 1, 9: 255. 1853.

Subgenus *Eucharis* affinis a qua imprimis differt floribus plerumque non pendulis, tubo perianthii bene infra fauce dilato, limbo plerumque minus expanso, ovario grandius et ovulis numerosis en quoque loculo.

Large bulbous perennial herbs. Leaves petiolate, persistent; lamina ovate, thin, plicate or ± smooth between the veins, undulate margined, apically acuminate, subcordate basally and shortly attenuate to the petiole, bright or dark green adaxially, light green abaxially, the abaxial epidermal cells variably striate; petiole subterete. Inflorescence scapose, umbellate, terminated by 2 green ovate-lanceolate bracts. Flowers subsessile or shortly pedicellate, 2–7, white, 7–8 cm long, strongly fragrant, declinate (rarely subpendulous), funnellform-campanulate (rarely crateriform); perianth tube cylindrical to subcylindrical below, abruptly dilated at 1/3–1/2 of its length, curved, tinged green below; limb of 6 ovate tepals in 2 series, imbricate for half their length, subequal, spreading somewhat above, often slightly undulate. Stamens basally connate into short or long staminal cup partially adnate to the upper portion of the tube, striped green or yellow within along the filamental traces, variously toothed or edentate; distal portion of the filaments linear or subulate, sometimes incurved; anthers linear, versatile at anthesis; pollen grain 40–60 μm (polar axis), 60–76 μm (longest equatorial axis), the exine coarsely reticulate. Style filiform, well-exserted beyond the staminal cup and slightly asurgent; stigma deeply trilobed, often green. Ovary large, ellipsoid, trigonous, appearing rostellate when dry; ovules usually 16–20 per locule, ellipsoid, biseriolate. Capsule green, seeds blackish brown with a slightly rugose testa (*E. moorei*).

Three species and two natural hybrids in western Colombia, Ecuador, and rarely Peru.

KEY TO THE SPECIES AND HYBRIDS
OF SUBGENUS *HETEROCHARIS*

- 1a. Leaves deeply plicate; staminal cup reduced to a basal connation of the filaments less than 7 mm long.
 - 2a. Staminal cup acutely bidentate between each filament, teeth ca. 1.5 mm long 1. *E. × grandiflora*
 - 2b. Staminal cup edentate or rarely with a single obscure tooth less than 1 mm long at the base of one or several stamens.
 - 3a. Perianth tube markedly curved, cylindrical for 1/2–2/3 of its length, then abruptly dilated distally to the throat; free filament somewhat incurved; stigmatic papillae unicellular 2. *E. sanderi*
 - 3b. Perianth tube straight or only slightly cernuous, subcylindrical proximally but distally dilating gradually towards the

throat; free filament straight; stig-
matic papillae multicellular

..... 3. *×Calicharis butcheri*

1b. Leaves shallowly plicate or relatively nonplicate; staminal cup well developed, greater than 1 cm long.

4a. Leaf length-to-width ratio usually equal to or less than 2; perianth more or less campanulate, tepals spreading only 45–60° from the throat; staminal cup acutely bidentate, strongly recurved at the margin; ovules 16–20 per locule; plants of Ecuador, very rare in Peru 4. *E. moorei*

4b. Leaf length-to-width ratio usually greater than 2; perianth crateriform, tepals spreading ca. 90° from the throat; staminal cup obtusely bidentate to quadrate, not strongly recurved at the margin; ovules 9–12 per locule; plants of the Huallaga valley in Peru

..... 5. *E. amazonica*

1. *Eucharis × grandiflora* Planchon & Linden, Fl. des Serres Jard. Eur. Ser. 1, 9: 255. 1853. *Urceolina grandiflora* (Planchon & Linden) Traub, Pl. Life 27: 57–59. 1971. LECTOTYPE (Meerow & Dehgan, 1984a): Fl. des Serres Jard. Eur. Ser. 1, 9: pl. 957. Figures 94–96.

Eucharis mastersii Baker, Curtis's Bot. Mag. 111: t. 6831. 1885. *Urceolina mastersii* (Baker) Traub, Pl. Life 27: 57–59. 1971. TYPE: ex hort. Sander (holotype, K; photo, F).

Eucharis lowii Baker, Gard. Chron. 13: 538–539. 1983. *Urceolina lowii* (Baker) Traub, Pl. Life 27: 57–59. 1971. TYPE: ex hort. Low (holotype, K; photo, F).

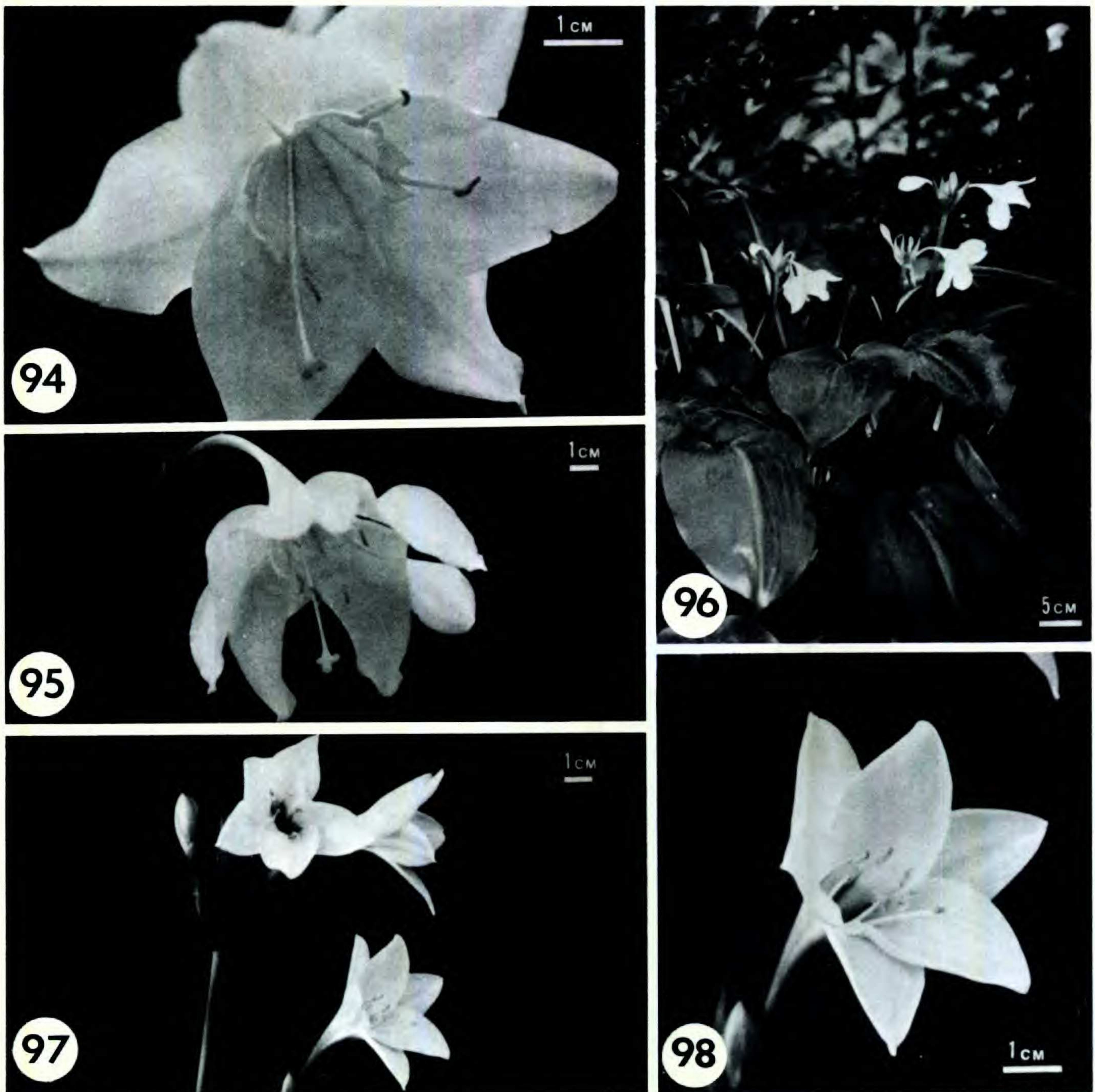
Bulb 3–5 cm diam., neck 2–4 cm long, tunics light brown. Leaves 1–3; petiole 19–36 mm long, 5–7 mm thick; lamina ovate or elliptic, 20–33 cm long, (10–)13–16 cm wide, apically acuminate, subcordate basally and shortly attenuate to the petiole, deeply plicate, adaxial surface lustrous dark or bright green, abaxial surface light green and densely striate, margins undulate. Scape 4–5 dm tall, 5–6 mm diam., subterete; bracts ovate-lanceolate, green at first, soon marcescent, 2.5–4.8 cm long, 14–17 mm wide. Flowers 2–6, funnel-form-campanulate, declinate, sweetly fragrant; pedicel short, 5–7(–10) mm long, 2.5–3.4 mm diam.; tube curved, 40–55 mm long, 1.5–2 mm wide below, dilating at ½–⅓ its length to 20–25 mm at the throat, green in the proximal half, white distally; tepals ovate, imbricate for half their length, white, margins usually undulate, spreading slightly apically; outer series (30–)35–40 mm long, (18–)20–26 mm wide, acute-apiculate; inner series 25–35(–40) mm long, 23–31 mm wide, obtuse. Staminal cup short, 5–7 mm long (to apex of teeth), 23–25 mm wide, stained green or yellow where

adnate to the dilated portion of the tube, with 2 acute or obtuse teeth between each stamen, teeth ca. 1.5 mm long; stamens (5–)6.7–7.5(–10) mm wide at the base from tooth to tooth; free filament 7–8.5(–10) mm long, linear or narrowly subulate, 1–1.5 mm wide at the base; anthers oblong-linear, 5.5–6.7(–7.5) mm long, slightly curved; pollen with only 10% stainability. Style filiform, (67–)74–85 mm long, green, assurgent, well exerted beyond the stamens, stigma deeply 3-lobed, 2.5–3.5(–5) mm wide, white or greenish. Ovary oblong, rostellate, 12–19 mm long, 6–8 mm wide; ovules 16–20 per locule, globose, superposed. Fruit and seed unknown, doubtfully ever formed. Chromosome number: $2n = 46$.

Distribution. Rare in the understory of primary and secondary rain forest of southern Chocó and northwestern Valle de Cauca departments of Colombia (Fig. 99), 80–600(–1,000) m elevation, but widely cultivated throughout western Colombia below 1,750 m. Rare and possibly introduced in Ecuador. The plant is functionally sterile. Most collections are from cultivation, and even seemingly native populations may be remnants of cultivation. Flowering at any time of the year.

Additional specimens examined. COLOMBIA. CHOCÓ: entre Istmina y Condoto, Río San Juan y Río Iro, 80–100 m, 5 Aug. 1944, *García-Barriga 11525* (COL, US). VALLE DE CAUCA: Río Cabrera, Tambi, Río Sumapaz, Cundinamarca, 600–1,000 m, Feb. 1883, *Lehmann 2644* (K); Cordova, Río Dagua, *Lehmann 2736* (K in part); Río Teta, Cauca Valley, 1,000 m, *Lehmann 7776* (F, GH, K, NY, US); Cauca, 1,000 m, *Lehmann s.n.* (K); cultivated 50 km SE of Buenaventura on old road to Pacific coast, Río Anchicaya, 500 m, 22 July 1984, *Meerow & Teets 1127* (FLAS). ECUADOR. CARCHI: Chical, path from Juan Maldonado to Tobar Danuso, flowered in cultivation, 23 Dec. 1982, *Madison et al. s.n.* (SEL). Guayas, Guayaquil, cultivated, Nov. 1925, *Mille 40* (QCA). Los Ríos, Hacienda Ana Maria, Canton Vinces, 60 m, *Y. Mexia 6644* (GH, US); vicinity Duran, cultivated, *Rose & Rose 23627* (US). EX HORT.: voucher of *Madison et al. s.n.*, Feb. 1983, *Meerow 1104* (FLAS).

Eucharis × grandiflora has long been confused with *E. amazonica* Linden ex Planchon (Meerow & Dehgan, 1984a). Meerow & Dehgan (1984a) re-established *E. grandiflora* (without hybrid designation) as distinct from *E. amazonica* in *Eucharis* subg. *Heterocharis*. At the time, I considered *E. lowii* and *E. mastersii* to be distinct but closely related to *E. × grandiflora*. In 1984, I collected material in Colombia referable to *E. lowii* Baker and received living material of *E. mastersii* collected in Ecuador. According to Baker (1893), who described these two species from cultivated material, *E. lowii* had a staminal cup half as long as



FIGURES 94–98. Natural hybrids of *Eucharis* subg. *Heterocharis*. 94–96. *E. × grandiflora*.—94. Flower of *E. “mastersii”* form (*Madison et al. s.n.*, SEL). 95, 96. *E. “lowii”* form (*Meerow & Teets 1127*, FLAS).—95. Habit in Colombia.—96. Flower. 97, 98. *× Calicharis butcheri* (*Meerow 1098*, FLAS).—97. Inflorescences.—98. Flower.

that of *E. “grandiflora,”* probably referring to *E. amazonica* or *E. moorei* (as *E. grandiflora* var. *moorei* Baker). When I compared the staminal cup of *E. lowii* with that of the lectotype of *E. × grandiflora*, the synonymy of *E. lowii* with *E. × grandiflora* became evident. The two seemed identical in all respects. Baker considered *E. lowii* to be a hybrid of *E. mastersii* and *E. “grandiflora”* and *E. mastersii* Baker (1885) to be a hybrid between *E. sanderi* and *E. “grandiflora.”* Baker distinguished *E. lowii* from *E. mastersii* merely by the former’s slightly longer-exserted staminal cup, which does not hold up. I now believe that *E. mastersii* and *E. lowii* are elements of a slightly variable hybrid taxon, *E. × grandiflora*, a putative hybrid

of *E. sanderi* and *E. moorei*. Though never collected in western Colombia, *E. moorei* does occur in contiguous northwestern Ecuador. It was likely a collection of this hybrid that Planchon & Linden (1853) described as *E. grandiflora*. *Eucharis × grandiflora* appears intermediate in all respects to *E. moorei* and *E. sanderi*. Virtually all collections of *E. × grandiflora* are from cultivated populations in Colombia and Ecuador according to specimen labels. Pollen stainability of either Colombian or Ecuadorean collections of *E. × grandiflora* is never better than 10%, and I have not succeeded in obtaining seeds in cultivation with either sibling pollen or pollen of other species. The hybrid is slightly variable in leaf morphology, num-

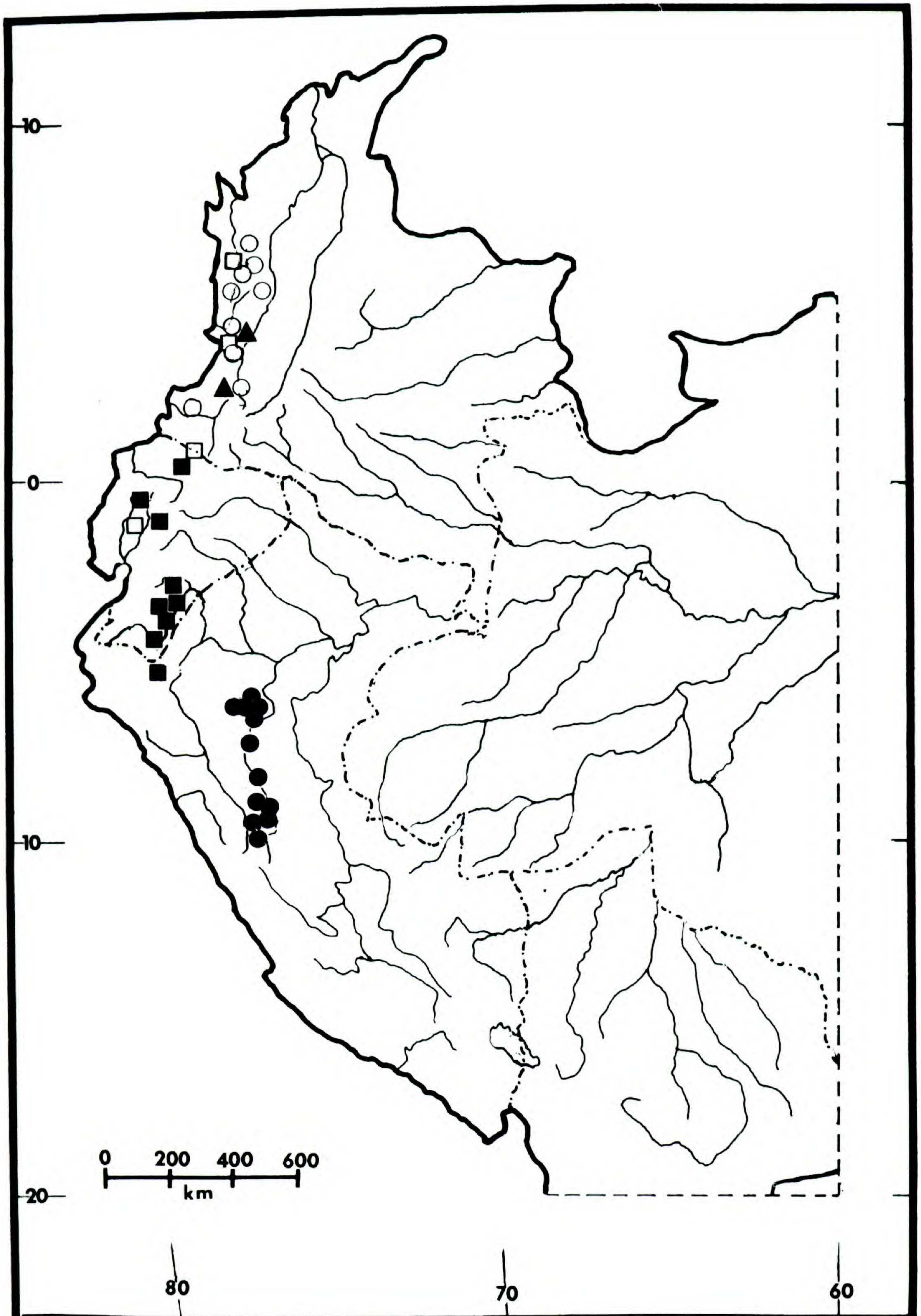


FIGURE 99. Distributions of species and hybrids of *Eucharis* subg. *Heterocharis* in northwestern-central South America. *Eucharis amazonica* (closed circles), *E. sanderi* (open circles), *E. moorei* (closed squares), *E. × grandiflora* (open squares) and *× Calicharis butcheri* (closed triangles).

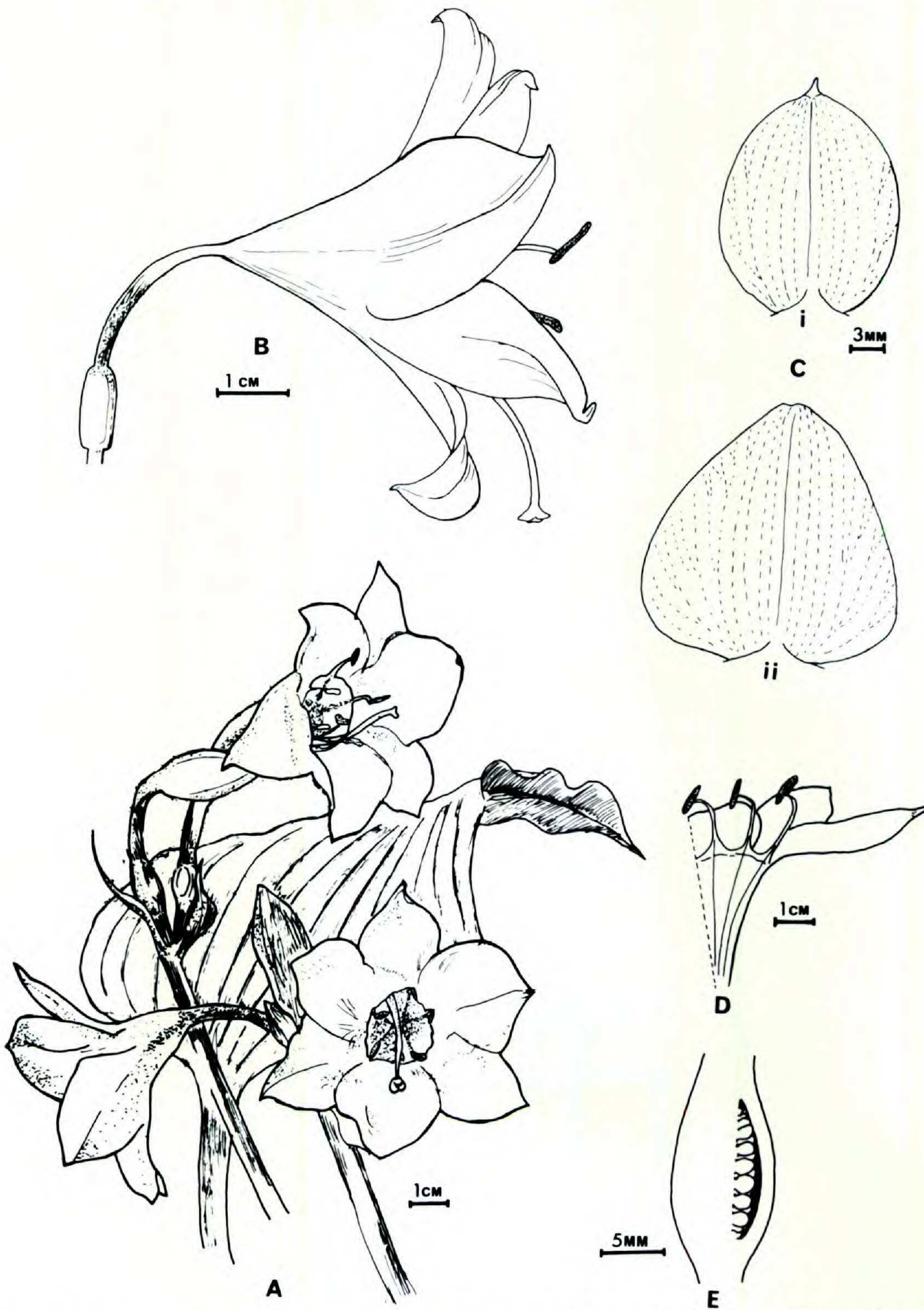


FIGURE 100. *Eucharis sanderi* (Cuatrecasas 16380, F).—A. Habit.—B. Flower.—C. Tepals. i, outer tepal; ii, inner tepal.—D. Detail of androecium.—E. Ovary, longitudinal section.

ber of flowers, and color of androecial pigmentation throughout its range, the extremes of which were recognized respectively as *E. mastersii* (Fig. 94) and *E. lowii* (Figs. 95, 96) by Baker (1885, 1893). The labels of all of Lehmann's collections indicate that they were prepared from material in Colombian gardens, and I encountered cultivated material referable to this hybrid in the Cauca valley and Pacific slopes of the Cordillera Occidental.

2. *Eucharis sanderi* Baker, Curtis's Bot. Mag. 109: t. 6676. 1883. *Urceolina sanderi* (Ba-

ker) Traub, Pl. Life 27: 57–59. 1971. TYPE: ex hort. (K). Figure 100.

Bulb 42.5–49 mm long, 32–47 mm wide; neck thick, 24–30 mm wide; tunics light brown. Leaves petiolate, persistent; petiole 31–50 cm long, 5.5–6(–8) mm thick; lamina ovate or elliptic, (23–)30–37 cm long, (10–)14–17 cm wide, thin, deeply plicate between the veins, undulate margined, apically acuminate, subcordate basally and shortly attenuate to the petiole, bright green adaxially, light green abaxially, the abaxial surface intensely striate.

Scape subterete, 45–54 cm long, 5–6 mm diam.; bracts lanceolate, 45–65(–77) mm long. Flowers 2(–3), subsessile (pedicels 5 mm or less long), strongly fragrant, declinate, funnelform-campanulate; perianth tube (45–)50–60(–70) mm long, cylindrical to subcylindrical and 2–3 mm wide below, abruptly dilated at ½ of its length to 20–27 mm wide, curved, tinged green proximally; tepals white, ovate, subequal, imbricate for half their length, spreading somewhat distally; outer series 26–32(–37) mm long, 16–20 mm wide, apiculate; inner series 24–30(–33) mm long, 20–25 mm wide. Stamens basally connate into a short staminal cup partially adnate to the upper portion of the tube, ca. 20–24 mm wide, striped green within along the filamental traces, only shortly exerted beyond the rim of the throat, edentate or rarely with one to few obscure teeth; free filaments (6–)7–9(–9.7) mm long, 1.8–2.2 mm wide at the base, linear, incurved; anthers (5.6–)6–8(–9) mm long linear, versatile, often curved; pollen grain 39.8 μm polar diam., 61.2 μm longest equatorial diam., the exine mostly coarsely reticulate. Style filiform, (66–)75–80(–90) mm long, well exerted beyond the staminal cup and slightly assurgent, white, sometimes flushed green; stigma deeply and obtusely trilobed, (2.8–)3–4 mm wide. Ovary large, ellipsoid, trigonous, appearing rostellate when dry, (10–)15–20 mm long, (5–)7–9(–11) mm wide; ovules (7–)10–20 per locule, ellipsoid, biseriate. Fruit and seed imperfectly known; capsule green; seeds several per locule.

Distribution. Endemic to western Colombia locally on sites with rich soil in the understory of wet, lowland rain forest, primarily in Chocó department (Fig. 99), frequently along watercourses; occasional in similar habitats in Valle de Cauca Dept., (5–)30–300(–1,000) m. Flowering may occur at any time of the year.

Additional specimens examined. COLOMBIA. CHOCÓ: headwaters of Río Tutunendo, E of Quibdo, 20–21 May 1931, *Archer 2197* (US); Municipio de San José del Palmar, Río Torito, 630–830 m, 5 Mar. 1980, *Forero et al. 6728* (MO); Río San Juan between Dipurdu & San Miguel, ca. 100 m, 14 Aug. 1976, *Gentry & Fallon 17687* (MO); Taparalito, Quebrada Taparal, N of Palestina, 4°15'N, 77°12'W, 30 m, 30 Mar. 1986, *Gentry et al. 53784* (FTG, MO); Corcovada region, upper Río San Juan, Yeracüi valley, 200–275 m, 24–25 Apr. 1939, *Killip 35276* (US); Andagoya, 70–100 m, Apr. 1939, *Killip 35401* (US). VALLE DE CAUCA: Río Calima, La Trojita, 5–50 m, 19 Feb.–10 Mar. 1944, *Cuatrecasas 16380* (F); Río Calima, Quebrada de La Brea, 30–50 m, 18–22 May 1946, *Cuatrecasas 21195* (F); Río Telembi, 12 Aug. 1880, *Lehmann 65* (G); Río Dagua, 0–300 m, 11 Aug. 1884, *Lehmann s.n.* (G). CAUCA: El Tambo, La Costa, 1,000 m, 3 July 1935, *von Sneidern 404* (S); El

Tambo, 800 m, 7 July 1936, *von Sneidern 1129* (S). CALDAS: Riseralda [?], Tatáma, Santa Cecilia [La Celia?], 800 m, 1 Dec. 1945, *von Sneidern 5208* (S).

This species is characterized by its large, sweetly fragrant funnelform-campanulate flowers, large ovaries and capsules, and reduced staminal cups. “Natural” hybrids exist between *E. sanderi* and both *E. “moorei”* (*E. × grandiflora*) and “*Caliphurria subedentata*” (*× Calicharis butcheri*). Despite the many putatively primitive characteristics of *E. sanderi* (e.g., large flowers, strong fragrance) in common with *E. moorei*, ovule number of *E. sanderi* is highly variable, and its leaves are deeply plicate. The reduced morphology of the androecium is the major advanced character of *E. sanderi*.

3. *× Calicharis butcheri* (Traub) Meerow, Nothogen. et comb. nov. *Eucharis butcheri* Traub, Pl. Life 23: 68. 1967. *Urceolina butcheri* (Traub) Traub, Pl. Life 27: 57–59. 1971. TYPE: ex hort. Traub, purported to have been collected in Panama by J. N. Giridlian, *Traub 1051* (holotype, MO). Figures 97, 98.

Eucharis sanderi Baker var. *multiflora* Baker, Curtis’s Bot. Mag. 111: t. 6831. 1885. *Eucharis sanderi* Baker subsp. *multiflora* (Baker) Traub, Pl. Life 23: 65. *Urceolina sanderi* subsp. *multiflora* (Baker) Traub, Pl. Life 27: 57–59. 1971. TYPE: Colombia. No other data, *Lehmann s.n.* (holotype, K).

Bulb 6–7 cm long, 3.8–5 cm wide, neck short and thick, tunics brown. Leaves 2–3; petiole 20–40 cm long, 5–6 mm wide; lamina elliptic, 21–26(–35) cm long, (10.5–)12–15 cm wide, shortly acuminate, subcordate-attenuate at the base, conspicuously plicate, adaxial surface bright to dark green, abaxial surface lighter green, the cuticle intensely striate. Scape 5–6 dm long, 4–5.5 mm diam.; primary bracts lanceolate, 41–57 mm long. Flowers 4–6(–7), funnelform-campanulate, fragrant; pedicels 4.5–5(–8) mm long; tube 35–42 mm long, funnelform proximally, dilating gradually from 1.5 mm wide at the base to 3.5 mm wide at median length, then abruptly dilated in the distal half to 13–16 mm wide at the throat, green for most of its length, the interior of the dilated portion stained green, most prominently along the filamental traces; tepals white, imbricate for half their length, spreading eventually to 45–55(–60) mm wide, margins nonundulate; outer series 20–28(–35) mm long, 12–17.5 mm wide, acute-apiculate; inner series 19–27(–32) mm long, 18–25 mm wide, obtuse. Stamens shortly connate below, edentate or rarely with one obscure tooth between some of the filaments, white; free filament linear,

straight or slightly curved apically, 6.7–8.7 mm long, 0.6–1 mm wide at the base where abruptly dilated to 2.5–3 mm; anthers (4.5–)6 mm long, linear-oblong, grayish brown, mostly devoid of pollen. Style 6–7 cm long, overtopping the stamens, slightly assurgent, white distally, green proximally; stigma obtusely trilobed, (2–)2.8–3 mm wide, papillae multicellular. Ovary globose-ellipsoid, 7.7–12(–15) mm long, (5–)7–9 mm wide; ovules 7–10(–12) per locule. Fruit and seed unknown, doubtfully ever formed. Chromosome number: $2n = 46$.

Distribution. Rare in western Colombia (Fig. 99), along the Río Dagua in Valle de Cauca Department, and the lower Cauca valley.

Additional specimens examined. COLOMBIA. VALLE DE CAUCA: Río Dagua, 17 Mar. 1883, *Lehmann 2736* (BM, K); Río Dagua, 200–500 m, *Lehmann 7774* (F, K in part). CAUCA: El Tambo, La Costa, 1,000 m, 24 June 1936, *Von Sneidern 1269* (S). PROVENANCE UNKNOWN: no data, Jan. 1938, *Cuatrecasas 1620* (F). EX HORT.: Kew acc. 430.53.43001, June 1984, *Meerow 1110* (FLAS).

This putative hybrid between *E. sanderi* and *Caliphruria subedentata* was first described by Baker (1885) as *Eucharis sanderi* var. *multiflora*. It has been collected in the wild at the interface of the distributions of both parents and at intermediate elevations. The plant produces little pollen, none of it staining with Alexander's (1969) stain. Floral morphology is intermediate between both parents, although, like *C. subedentata*, the stigmatic papillae are multicellular. There is some karyological evidence of hybrid intermediacy as well (Meerow, 1987b).

4. *Eucharis moorei* (Baker) Meerow, *Sida* 13: 29–49. 1987. *Eucharis grandiflora* var. *moorei* Baker, *Gard. Chron.* 4: 628. 1888. TYPE: ex hort., 1888, *Glasnevin s.n.* (K). Figures 101, 102.

Bulb 6–7 cm long, 2.5–4 cm diam., tunics brown. Leaves 2–3; petiole 2–4 dm long, 5–7 mm thick, with an anomalous arc of accessory vascular bundles near the adaxial surface; lamina broadly ovate, length/width ratio ≤ 2 , 17–30 cm long, 10–14 cm wide, apex shortly acuminate, base appearing cordate at the base, margins coarsely undulate, lustrous dark green adaxially, lighter green abaxially, abaxial cuticle mostly without striations. Scape 5–7 dm tall, terete, 7–10 mm diam. proximally, ca. 5 mm diam. distally; bracts ovate-lanceolate, (25–)35–45 mm long, green. Flowers usually 4, rarely up to 7, \pm campanulate, declinate, sweetly

fragrant; pedicels usually short, 3–10(–18) mm long; tube 40–52 mm long, cylindrical and 1.7–2 mm wide proximally, abruptly dilating at about its midpoint to (15.5–)18.5–25 mm at the throat, white except for a slight green tinge at the base; limb spreading less than 90° from the throat to ca. 70 mm wide or less; tepals ovate, the margins undulate; outer series 3.3–4 cm long; 17–22 mm wide, apiculate; inner series 2.9–3.8 cm long, 22–27 mm wide, obtuse. Staminal cup broadly cylindrical, (8–)10–15(–16.4) mm long (to apex of teeth), 20–25 mm wide, strongly recurved at the margins, white on the exterior, yellowish green on the interior, shallowly cleft between each stamen, bidentate between each free filament, teeth acute, 2.5–3 mm long; each stamen ca. 7–8 mm wide tooth to tooth; free filament subulate, (5–)6–8.5 mm long, 2 mm or less wide at the base; anthers 5.5–6.5 mm long, oblong-linear, grayish-brown; pollen grain ca. 48.6 μm polar diam., ca. 71.2 μm longest equatorial diam. Style 6–7 cm long; stigma 2.5–3.5 mm wide, white. Ovary ellipsoid-trigonal, (7–)10–13 mm long, ca. 5 mm wide; ovules 16–20, biseriate. Capsule globose, ca. 1.5 cm long, 1.3 cm wide, slightly rostellate, green, slightly glaucous; seeds 1–3 per locule, compressed globose, ca. 6 mm diam., turgid, testa blackish brown and slightly rugose. Chromosome number: $2n = 46$.

Distribution. An understory plant of primary and secondary lower montane rain forest of the Ecuadorean Andes (Fig. 99), in Morona-Santiago and Zamora-Chinchipec provinces on the east slopes, and Los Ríos, Cotopaxi, and contiguous Pichincha provinces on the western declivity, (220–)600–1,200(–1,600) m; rare in the “ceja de la selva” of Cajamarca Department, Peru. Flowering is concentrated January–March and again (June–) July–September.

Additional specimens examined. ECUADOR. COTOPAXI: km 52–53 on rd. from Quevedo to Latacunga, Río Pilalo, 800–950 m, 11 Aug. 1984, *Meerow & Meerow 1137* (FLAS); same locality, 13 Aug. 1984, *Meerow & Meerow 1141* (FLAS). GUAYAS: Guayaquil, cultivated, Nov. 1926, *Mille 40* (QCA). LOS RÍOS: km 56 Quevedo–Santo Domingo, Río Palenque Biological Station, 220 m, flowered in cultivation, *Dodson 5527* (SEL); same locality, 16 Oct. 1984, *Dodson & Dodson 15330* (MO). MORONA-SANTIAGO: 27 km SE of San Juan Bosco, 1,270 m, 27 Jan. 1981, *Gentry et al. 30913* (MO, SEL); Indanza-Limón (General Plaza), 1,300–1,600 m, 23 Mar. 1974, *Harling & Andersson 12779* (GB); 3 km N of Tucumbatza on road Gualaquiza–Indanza, 1,200 m, forest remnants, 19 Apr. 1985, *Harling & Andersson 24329* (GB); Río Yunganza, rd. Limón–Mendez (78°19'W, 2°49'S), 1,100 m, 23 Sep. 1979, *Holm-Nielsen et al. 20393 & 20407* (AAU); Río Gualaquiza and Río Bomboiza, E Andes of Sigisig, 800–1,200 m, *Lehmann 5882*

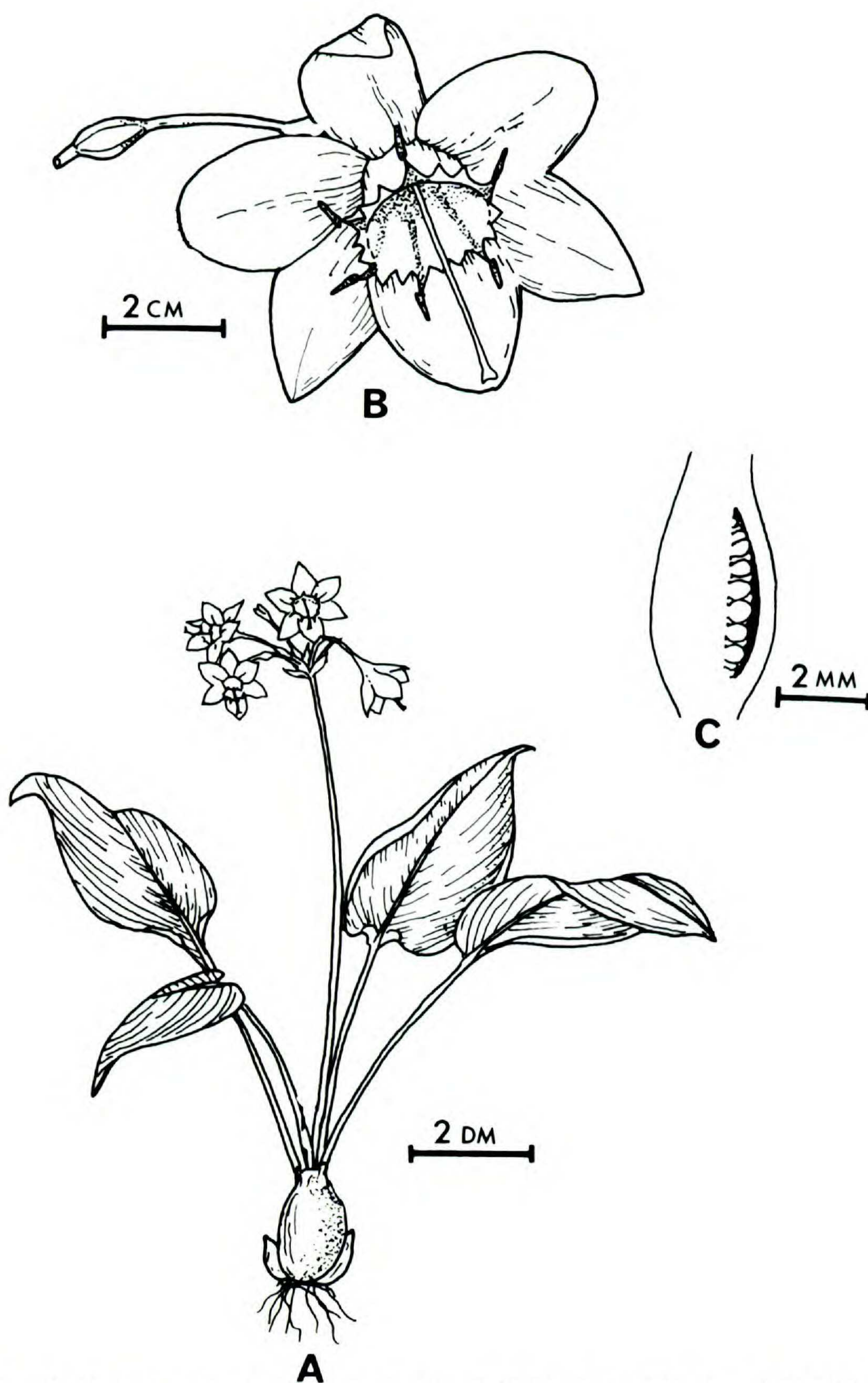


FIGURE 101. *Eucharis moorei*, after a drawing by Wendy B. Zomleffer of *Dodson 5527* (SEL).—A. Habit.—B. Flower.—C. Ovary, longitudinal section.

(K); 10–20 km from Gualaquiza on rd. to Sigües-Cuenca, 1,300 m, 5 Aug. 1984, *Meerow & Meerow 1135* (FLAS). PICHINCHA: Nanegal, W slope Andes, 5,000 ft., *Jameson 9* (G, P). ZAMORA-CHINCHIPE: Yurupaza, 600 m, 3 June 1947, *Harling 1407* (GB); W side Río Valladolid, 2,100–2,400 m, 15 Oct. 1943, *Steyermark 54717* (F). PERU. CAJAMARCA: Jaen, Río Tabaconas valley, 900–1,000 m, May 1912, *Weberbauer 6251* (GH, US).

Herbarium material of *E. moorei*, when first received, was assigned to *E. amazonica*. In 1984,

I collected the species on both sides of the Ecuadorean Andes. Morphological, anatomical, and karyological differences between these collections and the Peruvian *E. amazonica* became evident. *Eucharis moorei* is fully fertile, diploid ($2n = 46$), and of fairly wide distribution throughout Ecuador. The anomalous arc of secondary bundles that appear in petiolar transverse sections of *E. moorei*, and reduced, in *E. amazonica*, are not found in

any other species of the genus investigated. *Eucharis moorei* is putatively the most primitive species of the genus, and shares numerous plesiomorphic character states with other genera of "infrafamily" Pancratioidinae (e.g., large fragrant flower, short pedicels, and numerous ovules per locule). *Eucharis moorei* is the only species in the genus that occurs on both sides of the cordillera.

5. *Eucharis amazonica* Linden ex Planchon, Fl. des Serres Jard. Eur. Ser. 2, 2: 1216–1217. 1857. LECTOTYPE (Meerow & Dehgan, 1984a): Fl. des Serres Jard. Eur. Ser. 2, 2: t. 1216–1217. Figure 103.

Bulb 3.5–6 cm diam., neck 2.8–4.5 cm long, tunics brown. Leaves usually 2–4; petiole (15–)25–30(–50) cm long, 5.5–9 mm thick; lamina long-elliptic, (20–)30–40(–50) cm long, (10–)12–18 cm wide, length/width ratio usually greater than 2, acuminate, subcordate at the base and attenuate to the petiole, lustrous, dark green adaxially and shallowly or inconspicuously plicate, abaxial surface lighter green, cuticular striations obscure or largely absent, margins coarsely undulate. Scape 4.5–7(–8) dm tall, ca. 1–1.5 cm diam. proximally, ca. 5 mm diam. distally, terete; primary bracts (30–)35–58(–61) mm long, broadly ovate-lanceolate, green. Flowers (4–)5–6(–8), subpendulous, sweetly fragrant; pedicel (9–)10–15(–25) mm long; tube white throughout, curved, (41–)46–58 mm long, cylindrical below and 2–2.5 mm wide, dilating abruptly at $\frac{1}{3}$ length to (15–)18–21(–24) mm at the throat; limb white, spreading widely to 60–90 mm wide; tepals ovate, outer series 35–45(–50) mm long, 21–30 mm wide, apiculate; inner series 30–40(–45) mm long, 25–35 mm wide, acute. Staminal cup widely cylindrical, 11.2–13.8 mm long (to apex of teeth), (22–)28–30(–34) mm wide, margins slightly recurved, the interior stained green, particularly along the filamental traces, shallowly cleft between each stamen; stamens 7–8(–9.5) mm wide at the base, each with 2 obtuse teeth, one on each side of the subulate free filament, rarely subquadrate; teeth 2–3 mm long; free filament 6.5–8(–10) mm long, 2.8–3.4 mm wide at the base; anthers oblong-linear, 6–7(–8) mm long, grayish; pollen ca. 51.6 μ m polar diam., ca. 78.3 μ m longest equatorial diam. Style white, 66–78(–85) mm long, exerted 1–1.5 cm from the staminal cup, slightly assurgent; stigma deeply 3-lobed, 3–3.5 mm wide when receptive. Ovary oblong-ellipsoid, (8–)10–14 mm long, (4–)5–7.5(–8) mm wide, somewhat rostellate; ovules 9–12 per locule, superposed. Fruit and seed



FIGURES 102, 103. *Eucharis moorei* and *E. amazonica*.—102. *E. moorei* (Meerow & Meerow 1141, FLAS).—103. *E. amazonica* (Schunke 14179, FLAS).

imperfectly known, capsule reported to be green and the seed ellipsoid with a black testa. Chromosome number: $2n = 68$.

Distribution. An understory herb of lower and mid-montane rain forest of northeastern Peru, most prominently in the Huallaga valley in the vicinity of Moyobamba and Tarapoto (Fig. 99), 500–1,500 m. Widely cultivated throughout the warm tropics and as a house and greenhouse plant in the temperate zone. Occasionally adventive in the West Indies and probably elsewhere. Flowering at least twice per year, (May–)July–August(–September) and December–March.

Vernacular names. Amangais blanco, amangay, flor de cebolla, azuzena, Amazon lily, Eucharist lily.

Additional specimens examined. PERU. HUÁNUCO: Huánuco, Tingo María, 20 Aug. 1940, *Asplund 13214* (S); Huánuco, Tingo María, hwy. La Oroya–Tingo María,

Mar. 1977, *Boeke 1196* (NY); Leoncio Prado, Rupa Rupa, Las Palmas, km 18.5 a la carretera Tingo María-Huánuco, 756–800 m, 22 July 1984, *Schunke 14055* (F, FLAS, MO); Leoncio Prado, Rupa Rupa, Castillo Grande, al oeste de Tingo María, 24 July 1984, *Schunke 14057* (COL, F, FLAS, GH, K, MO, NY, UC, US); Huánuco Puerte Durand north of Huánuco, Río Chinchao valley, 7 Nov. 1938, *Stork & Horton 9880* (F, US); vicinity of Afilador, 670 m, *Woytkowski 101* (F). SAN MARTÍN: Lamas, Lamas, on trail from Tabalosos to Lamas, along Río Cumbaquiri, ½ hour W of Río Mayo, ca. 1,500 ft., 13–15 Sep. 1937, *Belshaw 3416* (F); near Uchiza, Huallaga valley, 500–550 m, 6 Aug. 1948, *Ferreyra 5154* (MO); Zepaelacio near Moyobamba, 1,200–1,600 m, Mar. 1934, *Klug 3559* (F, G, GH, K, NY, S US); Pachiza, Río Huayabamba, 1 Aug. 1959, *Mathias & Taylor 3974* (F); Roque, 9 Aug. 1925, *Melin 92* (S); between Balsapuerto and Moyobamba, 3,000 ft., *Sandeman s.n.* (BM); Lamas, Lamas, Fundo San Rafael, sector Santana, near Quebrada Chupishiña, 800 m, 5 Dec. 1984, *Schunke 14171* in part (FLAS); Moyobamba, 100[?]-1,100 m, *Weberbauer 4642* (G); Lamas, near Tarapoto, 840 m, Dec. 1929, *Williams 6348* (F, US); San Roque, 1,350–1,500 m, Feb. 1930, *Williams 7802* (F).

Meerow & Dehgan (1984a) re-established *Eucharis amazonica* distinct from *E. × grandiflora*, a taxon with which it has been confused since its description by Planchon (1857). The species is indigenous only to Peru, in the upper and middle Huallaga valley, but is grown worldwide in tropical regions and may be sporadically adventive. The species has a somatic chromosome number of $2n = 68$ (Meerow, 1987b; Nagalla, 1979) and is at least partially sterile. No specimen of *E. amazonica*, in contrast to most other species, has ever been collected in fruit; pollen stainability is only 50–65%; and viable seed has never been produced in cultivation. It is therefore conceivable that all populations of *E. amazonica* constitute a single clone. Its distribution throughout its narrow range may have been promoted by transient agriculturists. I believe *E. amazonica* to be a triploid-derived ($3x-1$) Peruvian isolate of either *E. moorei* or a possibly extinct mutual ancestor. The morphological differences between these taxa are cryptic and virtually impossible to discern in most dried material without dissection of the ovary. Their close relationship is further supported by the presence of secondary vascular bundles in the petiole of both taxa, although much smaller in *E. amazonica*.

DOUBTFUL OR EXCLUDED NAMES IN *EUCCHARIS*

Eucharis galanthoides hort., Linden, usually cited as *E. galanthoides* (Klotzsch) Linden (e.g., by Macbride, 1936; Traub, 1963), Ann. Cat. Hort. 17: 4. 1862. This combination is based on the erroneous assumption that Linden's *Eucharis galanthoides* was based on *Mathieua galanthoides*

(Klotzsch (Meerow, 1987a). The actual basionym was *Pancratium galanthoides*, a name under which Linden received material of a *Eucharis* collected by Gustav Wallis in Amazonas. *Mathieua galanthoides* was collected by Warscewicz in xeric, northwestern Peru (*Warscewicz s.n.*, B). No type has been located for Linden's plant, and the name *E. galanthoides* merely appeared as a listing in his catalog. It is likely referable to *E. castelnaeana* (Baillon) Macbride.

Eucharis himeroessa Sandwith ex Standley, *Herbertia* 3: 4. 1936. This name was never validly published with diagnosis or description. It was applied to a population of *E. bouchei* var. *bouchei* Woodson & Allen from San José Province in Costa Rica.

Eucharis paradoxa hort., T. Moore, Gard. Chron. 1: 242. 1876. A listed name, never described or illustrated, supposedly applied to the plant later described as *Caliphruria subedentata* Baker.

Pancratium galanthoides hort., Linden, Ann. Cat. Hort. 17: 4. 1862. See discussion under *Mathieua galanthoides*.

Caliphruria Herbert, Edwards's Bot. Reg. 30 (misc. no. 83): 87. 1844. *Urceolina* subg. *Caliphruria* (Herbert) Traub, Pl. Life 27: 57–59. 1971. TYPE SPECIES: *Caliphruria hartwegiana* Herbert.

Small bulbous perennial herbs. Leaves glabrous, petiolate, persistent or rarely hysteranthous; petiole subterete; lamina ovate, ovate-elliptic or elliptic, slightly succulent, apically acute or acuminate, basally attenuate to the petiole, margins nonundulate, dark green and smooth-surfaced adaxially, lighter green abaxially, the cuticle of the abaxial epidermis thickly striate or ridged, hypostomatic or with adaxial stomata only near and upon the midrib. Inflorescence scapose, umbellate; scape slender, terminating in 2 marcescent bracts enclosing the flowers before anthesis. Flowers pedicellate, (3–)5–10(–12) on thin pedicels, each subtended by a linear-lanceolate bracteole, declinate or subpendulous by the laxness of the pedicel, 2–4 cm long, without noticeable fragrance, white, funnellform or funnellform-tubular, protandrous; perianth tube funnellform, dilating gradually from the base, tinged green below, or subcylindrical and white throughout, straight; limb of 6 lanceolate, ovate or elliptic tepals in 2 subequal series, the segments imbricate for half their length, diverging in their distal half. Stamens connate only at the base, forming a short,

membranaceous staminal cup, variously toothed or edentate between each filament, distal portion of the filament narrowly subulate or linear, subequal; anthers oblong, erect at anthesis, eventually versatile; pollen grains medium-sized (longest equatorial axis ca. 50 μm), the exine finely reticulate. Style filiform; stigma trilobed, papillae multicellular. Ovary globose, green, with septal nectaries; ovules ellipsoid, (1-)2-7 per locule, medially superposed, placentation axile. Fruit a thin-walled, leathery, yellow-green, loculicidal capsule; seeds few per locule; globose or compressed-ellipsoid, ca. 3-5 mm long, testa black or brown. Chromosome number: $2n = 46$.

Four species, three endemic to western Colombia, one to Peru.

KEY TO THE SPECIES OF *CALIPHRURIA*

- 1a. Perianth more than 2 cm long; tube 9 mm or more long.
 - 2a. Perianth tube 9-13.5 mm long; stamens 5.8-6.8 mm long, bidentate between each stamen, length of teeth at least $\frac{1}{2}$ the length of the free filament 1. *C. hartwegiana*
 - 2b. Perianth tube 15-25 mm long; stamens 9 or more mm long, edentate or occasionally with 1-2 teeth between each stamen, teeth never more than $\frac{1}{10}$ the length of the free filament 2. *C. subedentata*
- 1b. Perianth equal to or less than 2 cm long; tube less than 9 mm long.
 - 3a. Leaves hysteranthous; perianth tube funnelform; stamens less than 5 mm long, more or less fasciculate, bidentate, teeth much exceeding the free filament in length, free filament 1-2 mm long, ovules 1-2 per locule 3. *C. tenera*
 - 3b. Leaves persistent; perianth tube subcylindrical; stamens 7-10 mm long, divergent, edentate, free filament 7-9 mm long, ovules 4-5 per locule 4. *C. korsakoffii*

1. *Caliphruria hartwegiana* Herbert, Edwards's Bot. Reg. 30, misc. no. 83: 87. 1844. *Eucharis hartwegiana* (Herbert) Nicholson, Illus. Dict. Gard. 1884. *Urceolina hartwegiana* (Herbert) Traub, Pl. Life 27: 57-59. 1971. The species as described by Herbert from Hartweg collections made near Guaduas, Colombia, lacks a holotype, and I have not located any specimen which could be designated as lectotype. The following neotype is herein proposed. NEOTYPE: Colombia. Huila: Río Magdalena near Paicol, 600-1,200 m, *Lehmann 6376* (neotype, K). Figure 104B.

Bulb globose with a brown tunic, ca. 32.8 mm diam., often apically articulated into a slender neck

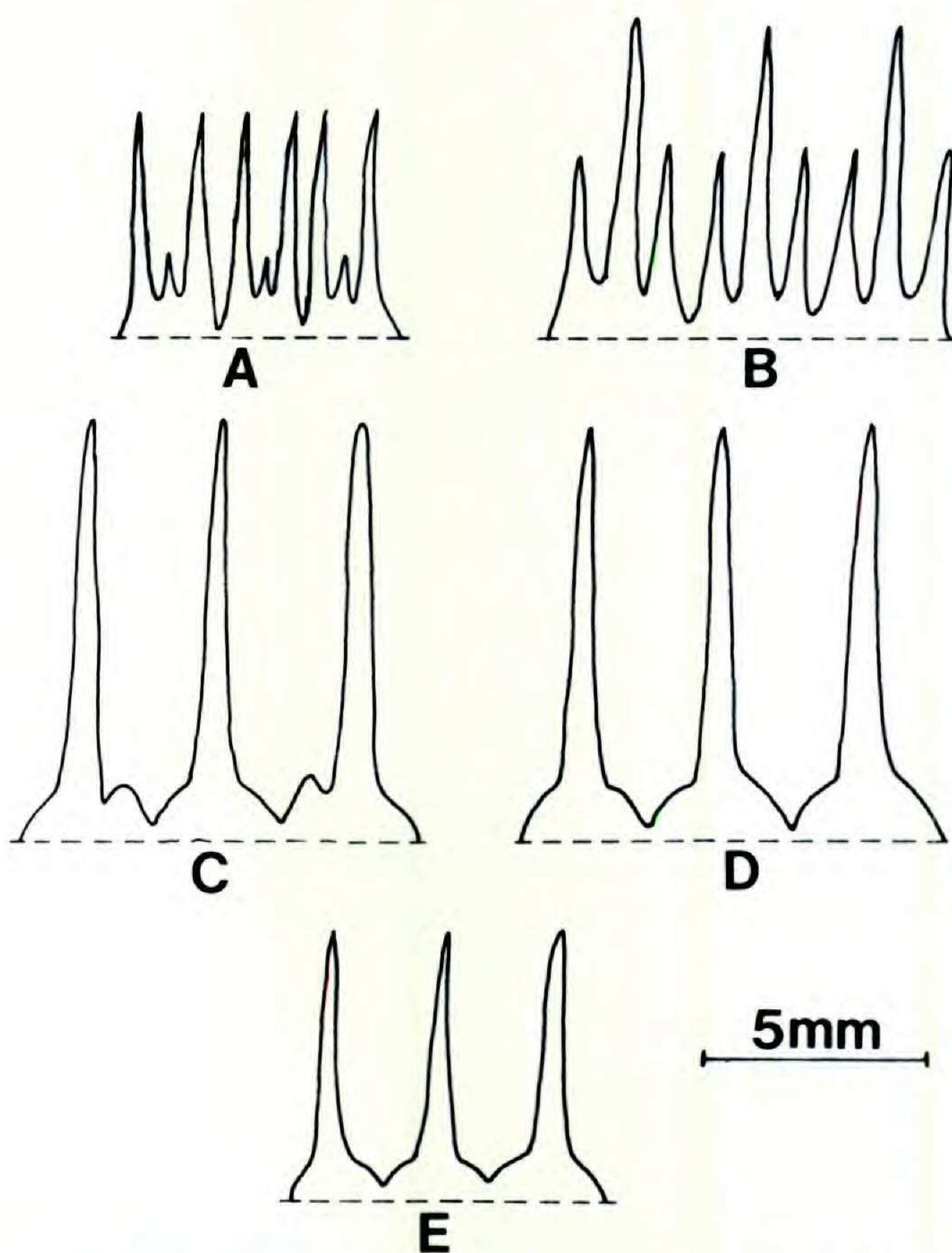


FIGURE 104. Androecial morphology of *Caliphruria* species.—A. *C. tenera* (*Triana 1289*, COL).—B. *C. hartwegiana* (neotype, *Lehmann 6376*, K). C, D. *C. subedentata*.—C. *Pittier 1009* (US).—D. Holotype, ex hort. *Beaufoy s.n.* (K).—E. *C. korsakoffii* (*Meerow 1096*, FLAS).

to 19.6 mm long. Leaves 2-4; petiole 13 cm long, 2.5-4.4 mm thick; lamina ovate to elliptic, 10-14 cm long, 3.8-6.3 cm wide, acuminate, shortly attenuate to the petiole at the base. Scape 28-31 cm tall; bracts lanceolate, 13.5-16.8 mm long and ca. 3 mm wide at the base; inner bracteoles successively smaller and narrower. Flowers 5-7; pedicels 12.8-15.8 mm long, thin; perianth 19-26 mm long, white, except for the proximal $\frac{1}{3}$ - $\frac{1}{2}$ of the tube, this green; tube funnelform, dilating gradually from the base, 9-13.5 mm long, ca. 2-3 mm wide at the base, 5-6 mm wide at the throat; limb spreading to 7.5-11 mm; tepals ovate-elliptic, the outer series ca. 14.8 mm long, 3.4 mm wide, acute-apiculate, the inner series ca. 12 mm long, 5 mm wide, obtuse. Stamens 5.8-6.8 mm long, narrowly subulate for most of their length, dilated to ca. 2.5 mm basally where connate, bidentate between each free filament; teeth ca. $\frac{1}{2}$ the length of the free filament; free filament ca. 1.5 mm wide at point of insertion to cup; anthers 5.2-5.4 mm long, linear, versatile. Style 25 mm long, exerted ca. 2.4 mm beyond the limb; stigma 1.8 mm wide; ovary globose, 2.8-3.1 mm diam.; ovules 2-3 per locule, axile, medially superposed. Mature fruit and seed unknown.

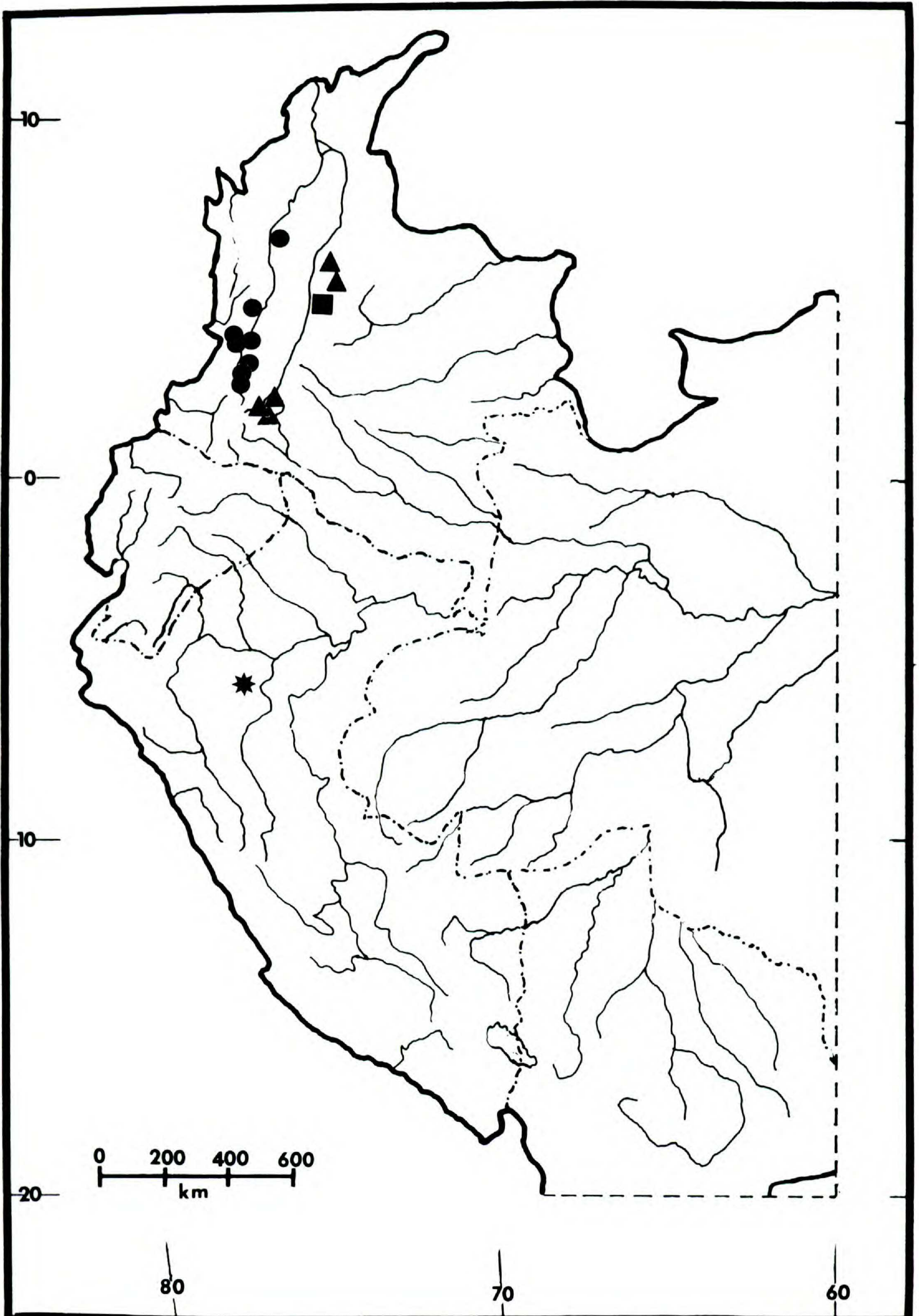


FIGURE 105. Distribution of species of *Caliphruria* in northwestern-central South America. *Caliphruria hartwegiana* (triangles), *C. korsakoffii* (star), *C. subedentata* (circles), and *C. tenera* (square).

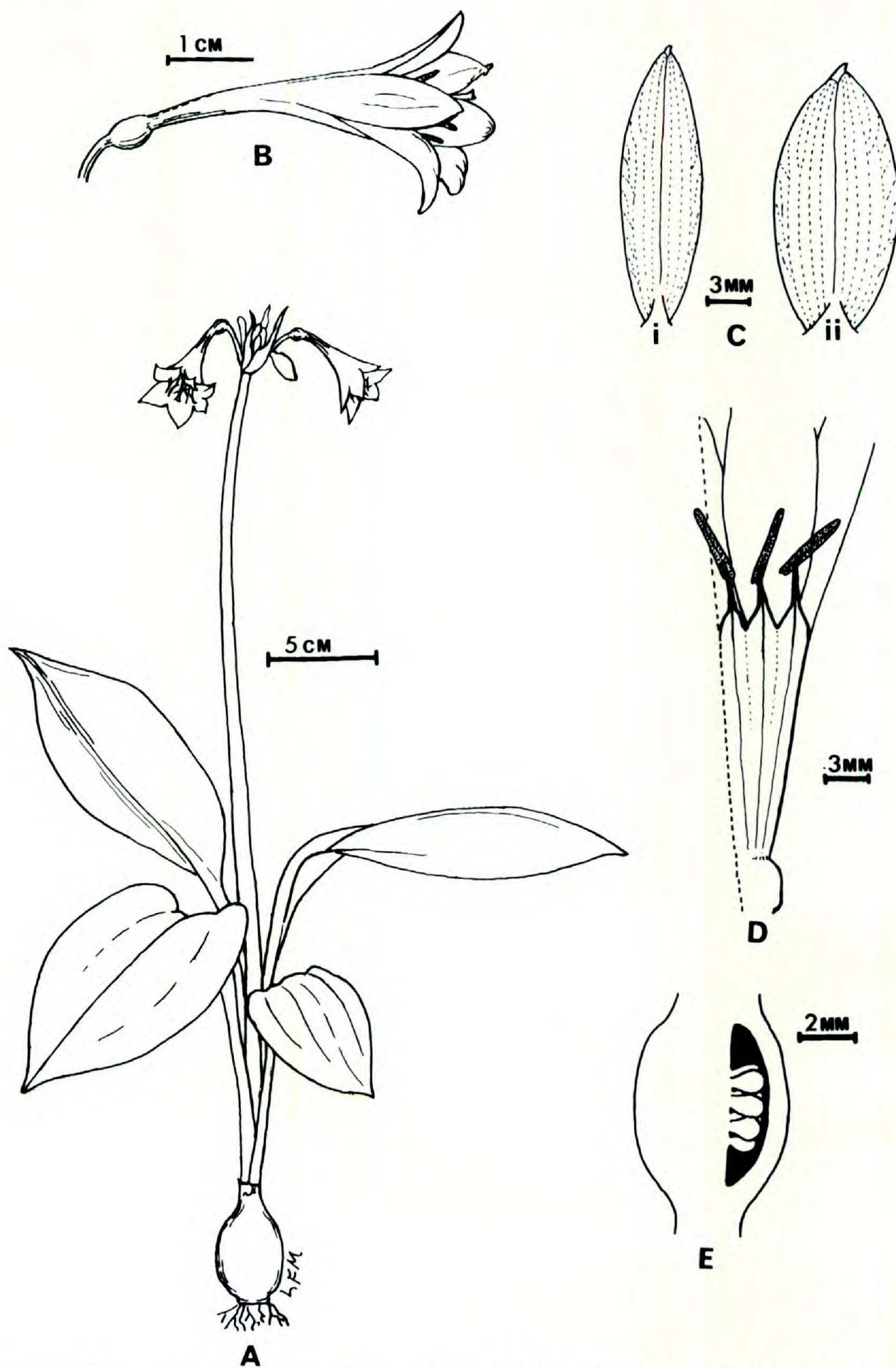


FIGURE 106. *Caliphruria subedentata* (Meerow 1123, FLAS).—A. Habit.—B. Flower.—C. Tepals. i, outer tepal; ii, inner tepal.—D. Longitudinal section through part of flower to show detail of androecium.—E. Ovary, longitudinal section.

Distribution. Rare in western-central Colombia, in the understory of montane forests of the Río Magdalena Valley (Fig. 105), 600–2,350 m.

Additional specimens examined. COLOMBIA. CUNDINAMARCA: Caparrapi, 1,275 m, 8–13 June 1939, *García-Barriga* 7713 (COL). EX HORT.: s.n. (K); 1882, s.n. (GOET). HUILA: forest around Finca Mehrenberg, 2,350 m, 6 July 1984, *D'Arcy et al.* 15634 (MO); Municipio de La Plata, Vereda Agua Bonita, Finca Meren-

berg, 1,200–1,300 m, 15 July 1975, *Díaz et al.* 534 (COL).

This seldom-collected species is distinguished from *C. subedentata* by its smaller flowers and short stamens with long teeth interposed between the filaments (Fig. 104B).

2. *Caliphruria subedentata* Baker, Curtis's Bot. Mag. 103: t. 6289. 1877. *Eucharis sub-*

edentata (Baker) Bentham & Hooker, *Genera Plantarum* 2: 731. 1883. *Urceolina subedentata* (Baker) Traub, *Pl. Life* 27: 57–59. 1971. TYPE: ex hort. *Beaufoy s.n.* (holotype, K; photo of type, COL). Figure 106.

Eucharis fosteri Traub, *Pl. Life* 7: 36. 1951. *Urceolina fosteri* (Traub) Traub, *Pl. Life* 27: 57–59. 1971. TYPE: Colombia. Cauca: above Cali on road to Buenaventura, 2,000 ft., collected by M. B. Foster, 5 Dec. 1946, *Traub 17* (holotype, MO).

Bulb globose-subglobose with a brown tunic, 22–45(–63) mm long, 20–32 (–44.5) mm wide, often apically articulated into a slender neck 11.8–23.5 mm long and 10–15.7 mm wide, offsetting vigorously. Leaves 2–4; petiole 10–28(–37) cm long, 4–7 mm thick; lamina ovate, ovate-elliptic, or elliptic, 14.5–19.5(–21) cm long, (4.5–)7–10 cm wide, acuminate, shortly attenuate to the petiole. Scape 25–40 cm tall, slender, 2.5–5.5 mm diam.; bracts 13–25.5(–30.5) mm long, 3–5.2 mm wide at base; inner bracteoles 5–14 mm long. Flowers (3–)5–7(–8); pedicels (13.6–)15.2–28(–44.3) mm long, thin, ca. 1 mm diam.; perianth (24–)31.6–39(–44.8) mm long, white except for the distal $\frac{1}{3}$ – $\frac{1}{2}$ of the tube, this green; tube funnellform, dilating gradually from the base, 15–25 mm long, ca. 2 mm wide at the base, 5–8 mm wide at the throat; limb spreading to 12.5–21 mm wide, tepals ovate-elliptic; outer series (15–)17.5–22.5 mm long, 5–8 mm wide, acute-apiculate; inner series (13.5–)15.8–20 mm long, 7–10 mm wide, obtuse and minutely apiculate. Staminal cup less than 1 mm long, edentate, rarely with 1–2 small teeth between all or some of the filaments, white; filaments narrowly subulate-linear for most of their length, (8–)9–11.5(–14.6) mm long, dilating to 1.5–2.5 mm at their point of insertion; tooth, when present, 1 mm or less long; anthers (5–)6.2–7 (–7.5) mm long, linear; pollen grain ca. 39.3 μ m polar diam., ca. 50.9 μ m longest equatorial diam. Style (28.9–)30–40(–45) mm long, exerted 4–6 mm beyond perianth, white; stigma 3-lobed, 1–1.5(–2.5) mm wide. Ovary globose-ellipsoid, 3–5 mm long, 2.5–5 mm wide; ovules (2–)3–5(–7) per locule, axile, superposed. Capsule ca. 1 cm diam.; seeds 1–2 per locule, compressed-ellipsoidal, 5–7 mm long, ca. 3–5 mm diam.; testa black, rugose.

Distribution. Understory of lower and middle montane forests of western Colombia in the cordilleras Occidental and Central, chiefly in the Río Cauca valley (Fig. 105), (760–)1,100–1,800 (–2,000) m. Flowering at any time of the year.

Additional specimens examined. COLOMBIA. CAUCA: Santander de Quilichao; selva densa en “Río Chiquito,”

2,000 m, 6 Oct. 1954, *Fernandez 2795* (COL); Río Cauca, 1,400 m, Sep. 1881, *Lehmann 939* (BM, G); Caloto, 1,200–1,500 m, June 1883, *Lehmann 2885* (G); Quebrada Guatica, 1,800 m, *Lehmann 3269* (K); Cajamarca, *Lehmann s.n.* (K); Caloto, 1,200–1,500 m, June 1880, *Lehmann s.n.* (K); along Río La Paila above Corrinto, Central Cordillera, 1,400 m, 19 Jan. 1906, *Pittier 1009* (US); vicinity of Medellín, 23 Mar. 1927, *Toro 111* (NY). VALLE DE CAUCA: Río Dagua Valley, La Margarita, ca. 760 m, Apr. 1939, *Killip 34872* (US); “La Manuelita,” Palmira, 1,090–1,100 m, May 1922, *Pennell & Smith 6182* (US). EX HORT.: 3 Apr. 1906, *Dammer s.n.* (B, GH photo); Bailey Hortorium BH 71-813, May 1982, *Meerow 1097* (FLAS); Bailey Hortorium BH 76-467, June 1984, *Meerow 1109* (FLAS); Huntington Botanical Garden HUNT 44356, June 1984, *Meerow 1123* (FLAS); Bailey Hortorium BH 60-777, July 1985, *Meerow 1153* (FLAS); ex hort. Bull, *s.n.* (K); ex hort. Linden, *s.n.* (K).

Caliphruria subedentata is the most common and variable species of *Caliphruria*, at one time found throughout the moist lower and middle montane forests of the slopes of the cordilleras Central and Occidental west of 76°W longitude (Fig. 105), and chiefly those surrounding the Cauca Valley. Much of this forest type has been destroyed in western Colombia so the species is no longer abundant. In the course of fieldwork in western Colombia in 1984, I was not able to find *C. subedentata* in its historical localities nor in the remnants of lower and middle montane forest that I explored. The species may yet persist in more inaccessible forested sites. Living material received from Mr. Thomas Fennell was said to have been collected in Ecuador, but this information is undocumented. At present, I have seen no Ecuadorean specimens of *Caliphruria*, nor encountered populations in the field.

Within the range of *C. subedentata*, variation in leaf size, flower size, dentation of the androecium (Fig. 104C, D), and number of ovules is evident, but these patterns are for the most part continuous and/or mosaic in distribution, rendering recognition of subspecific taxa inappropriate. Though Baker (1877) characterized the species by the presence of one or two small teeth between the free filaments, the flowers present on the type specimen of *C. subedentata* are completely edentate. Clonotypic material of the taxon described by Traub (1951) as *E. fosteri* is distinguishable from other living material of *C. subedentata* only by its slightly smaller leaves and flowers.

3. *Caliphruria tenera* Baker, *Handbook of the Amaryllideae*, p. 112. 1888. *Eucharis tenera* (Baker) Traub, *Pl. Life* 23: 65. 1967. *Urceolina tenera* (Baker) Traub, *Pl. Life* 27: 57–59. 1971. TYPE: Colombia. Río Magda-



FIGURE 107. *Caliphruria korsakoffii* (Meerow 1096, FLAS).

lena, Aug. 1844, *Goudot s.n.* (holotype: K; isotype: P).

Bulb globose or ellipsoid, ca. 25 mm diam. or 30 mm long \times 17.5 mm wide, sometimes apically articulated into a short neck 10 mm long \times 5 mm wide; tunic grayish brown or tan. Leaves hysteranthous, not seen. Scape terete, slender, 16–27 cm tall, 1–2 mm diam.; bracts linear-lanceolate, 17–28.3 mm long; inner bracteoles linear, the longest to 14.5 mm. Flowers 5–10; pedicels 14–23.2 mm long, thin; perianth 17–19 mm long, funnellform, white; tube 8.5–9.5 mm long, funnellform, dilating gradually from 1.3 mm wide at the base to 3–4 mm at the throat; limb spreading to 15.5 mm; tepals ovate to elliptic, the outer series 8.5–11.2 mm long, 2–2.5 mm wide, acute-apiculate; the inner series 8–10 mm long, 2.8–3.8 mm wide, obtuse. Stamens 3–5 mm long, each stamen bidentate, 1.5–2.2 mm wide, the free filament inserted between the teeth; teeth much exceeding the free filament, 3–4 mm long; free filament 0.8–1.5 mm long, linear; anthers 4–5.5 mm long, linear; pollen grain ca. 35.2 μm polar diam., 53.7 μm longest equatorial diam. Style 18–21 mm long; stigma 3-lobed, 1 mm wide. Ovary globose, 1.8–2.7 mm diam.; ovules 1–2 per locule, axile, medially superposed. Fruit and seed unknown.

Distribution. Colombia, valley of the Río Magdalena (Fig. 105), 400 m.

Additional specimen examined. COLOMBIA. CUNDINAMARCA?: "Prov. Bogota," Copo la Parada, 400 m, July 1853, *Triana 1289* (COL, US, photo GH).

Caliphruria tenera is the smallest-flowered Co-

lombian representative of *Caliphruria*. It is readily distinguished by its hysteranthous leaves and the long teeth of the androecium which greatly exceed the short free filament (Fig. 104A). Unfortunately, *C. tenera* has not been re-collected since 1853. The hysteranthous leaves of this species suggest adaptation to drier habitats than usually characteristic of the genus. Pockets of xeric vegetation do occur in the vicinity of the type locality (Cuatrecasas, 1958).

4. *Caliphruria korsakoffii* (Traub) Meerow, comb. nov. *Eucharis korsakoffii* Traub, *Pl. Life* 23: 85–87. 1967. *Urceolina korsakoffii* (Traub) Traub, *Pl. Life* 27: 57–59. 1971. TYPE: Peru. San Martín: 40 km from Moyobamba, Hierra waterfalls, 1,500 m, ex hort. J. N. Giridlian from bulbs collected by Lee Moore, 16 July 1966, *Traub 1060* (holotype, MO). Figure 107.

Bulb \pm globose, 31 mm long, 29.3 mm wide, without an appreciable neck, tunic brown, offsetting weakly. Leaves 2–4; petiole 4.5–10 cm long, 3–4 mm thick; lamina ovate-lanceolate to narrowly elliptic, 13–17 mm long, 3.3–4.8 mm wide, acute-acuminate, basally attenuate to the petiole, cuticle of the abaxial epidermis thickly ridged. Scape 15–25 cm tall, 3.5–3.7 mm diam.; bracts lanceolate, 19–25 mm long, 5.5 mm wide at the base; inner bracteoles 8.5–22 mm long. Flowers 10–12, 15–20 mm long, funnellform, white, declinate to slightly ascendent; pedicels 2–4 cm long; tube subcylindrical, straight, 4–6 mm long, 2 mm wide at base, 3.2 mm wide at throat; limb spreading to ca. 2

cm; outer tepals lanceolate, 10–18.5 mm long, 4–5 mm wide, acute-apiculate; inner tepals ovate, 7.5–16 mm long, (5–)7–8 mm wide, obtuse and minutely apiculate. Stamens (7–)9.5–10 mm long, 0.7 mm wide at the base, edentate, diverging distally, narrowly subulate, white; anthers 3–4 mm long, oblong, dorsifixed in lower third, versatile; pollen grain ca. 32.3 μm polar diam., 50.4 μm longest equatorial diam. Style 16–21 mm long, white, slightly longer than limb segments; stigma 3-lobed, (1.2–)2.5–2.7 mm wide. Ovary globose-ellipsoid, 3.5–5 mm long, 2–3 mm wide; ovules 4–5 per locule, medially superposed. Capsule ca. 1 cm diam., yellow-green, thin-walled; seeds 1 per locule, globose, ca. 3 mm diam., testa brown. Chromosome number: $2n = 46$.

Distribution. North-central Peru (Fig. 105) at 1,500 m. Known only from the type locality in the understory of dense lower montane rain forest in humic topsoil on steep slopes, often growing wedged in the crevices of rocks.

Additional specimens examined. EX HORT.: Clone of type collection, *s.n.* (K); clone of type collection, July 1964, *Traub s.n.* (MO); clone of type collection, May 1982, *Meerow 1096* (FLAS).

Caliphruria korsakoffii is the only species of *Caliphruria* presently known outside of Colombia. In the size of the flower this species has affinity with *C. tenera* but can be distinguished by having evergreen leaves, subcylindrical tubes, and edentate, divergent, and longer stamens (Fig. 104E), coarser pollen exine reticulation, more numerous ovules, and higher altitudinal limits. The seeds of *C. korsakoffii* have a brown testa; those of *C. subedentata* are black. The ridged cuticle of the abaxial leaf surface of *C. korsakoffii* (Fig. 12) is quite different from the narrow cuticular striations of *C. subedentata* (Fig. 11). The morphological novelties exhibited by *C. korsakoffii* suggest considerable isolation from the Colombian taxa of *Caliphruria*.

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